

PULSATILE PRESSURES IN THE CRANIAL FLUIDS OF *HETERODONTUS PORTUSJACKSONI*

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It has been shown in mammals (Hamilton, Woodbury & Harper, 1936, 1944) that dilation of the craniospinal blood vessels by the pressure pulses caused by straining and coughing is largely prevented by the direct communication of the raised intrathoracic pressure to the cerebrospinal fluid (CSF). The pathways through which pressure is communicated include the loose areolar tissue around the spinal nerves, and the venous blood in the paravertebral plexuses which communicate with the large veins at the back of the thorax and abdomen. McIntosh, Estes & Warren (1956) have shown by means of myelograms that as the intrathoracic pressure rises, the spinal nerves move medially and the subarachnoid space narrows.

The Port Jackson shark, *Heterodontus portusjacksoni* exhibits spontaneous, rhythmic, and evoked coughing during which the pharynx is contracted and water is forced from the mouth and gill slits (Satchell & Maddalena, 1972). During an evoked cough water pressure in the pharynx may exceed 70 cm H₂O; this is more than thirty times that of normal respiration. Some preliminary observations indicated that here too the rise of pressure in the pharynx is communicated via the dorsal aorta to the craniospinal vessels, and, by some more direct route to the fluid surrounding the brain. The totally different anatomy of the respiratory system of a fish compared with that of a mammal suggested that the phenomenon required investigation.

MATERIAL AND METHODS

Port Jackson sharks were captured in the vicinity of Sydney harbour and maintained at the Marineland Oceanarium until required. Twenty-three adult specimens ranging from 5 to 13 kg were used. In the laboratory they were fixed in a stainless-steel tank by clamps on their brow ridges and fin spines. Aerated filtered water was circulated through the tank; temperatures were maintained at 19 ± 1 °C.

Extrabrain fluid pressures were recorded from a polyethylene cannula ending in a No. 16 hypodermic needle inserted into the cranial cavity rostral to the cerebrum. Orobranchial pressures were recorded from the spiracle with a No. 19 needle having a lateral opening. Dorsal aortic blood pressure was recorded from a polyethylene cannula inserted into the dorsal aorta at the amputated tip of the tail. All three cannulae led to Statham P23BB or P23GC pressure transducers. The manometers were

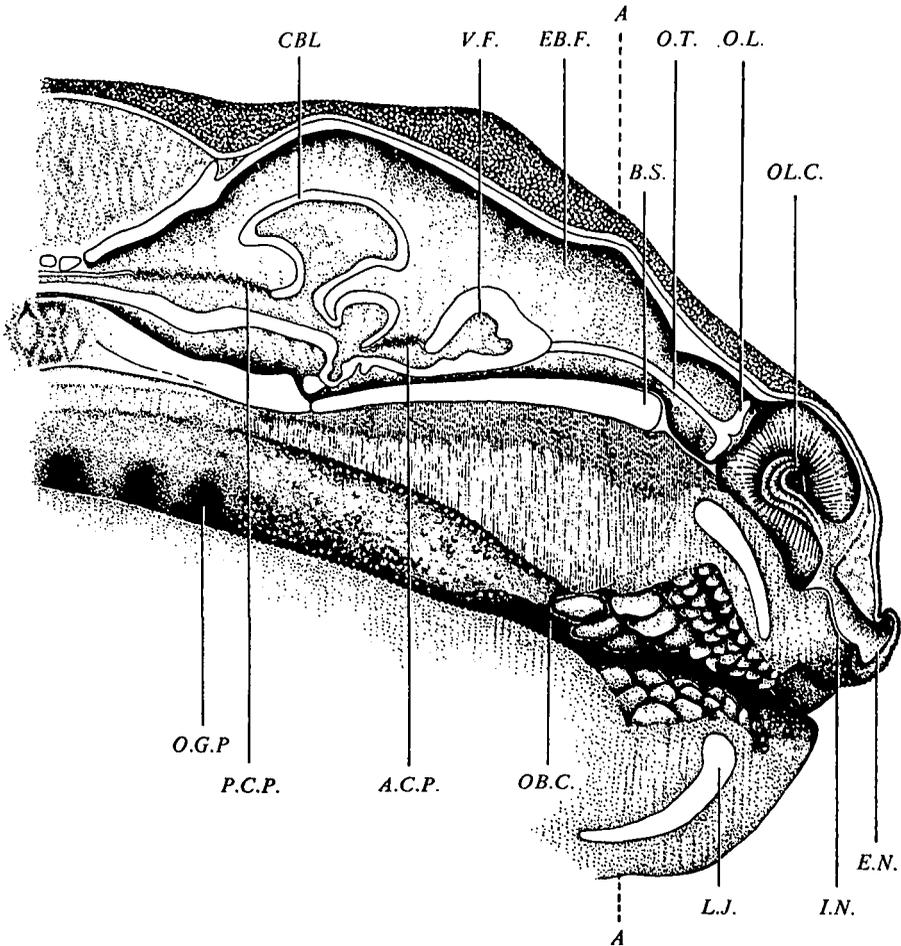


Fig. 1. Longitudinal section through the head of a Port Jackson shark. At level *A-A*, section angled to pass through olfactory capsule. *A.C.P.* anterior choroid plexus, *B.S.* base of skull, *CBL* cerebellum, *EB.F.* extrabrain fluid, *E.N.* external nares, *I.N.* internal nares, *L.J.* lower jaw, *OB.C.* orobranchial cavity, *O.G.P.* opening of gill pouch to orobranchial cavity, *O.L.* olfactory lobe, *OL.C.* olfactory capsule, *O.T.* olfactory tract, *P.C.P.* posterior choroid plexus, *V.F.* ventricular fluid.

repeatedly calibrated using the water surface as zero reference pressure. Records were presented on a Grass 4-channel polygraph.

Fish were usually set up on the afternoon of one day and were left overnight. Spontaneous coughing commonly commenced by the following morning. Evoked coughs were produced by lightly irritating the nares, the lips, the roof of the mouth, or the gill flaps with a probe.

RESULTS

Anatomy

In the skull a large fluid-filled cavity separates the meninx primitiva from the vascularized lining of the cranial cavity, the endorachis (Ariëns Kappers, 1926). Within the ventricles of the brain and in the spinal canal is the ventricular fluid, VF.

It resembles the cerebrospinal fluid of mammals in that it lacks all but a trace of protein and is produced by the choroid plexuses at much the same rate as mammalian CSF, if allowance is made for the difference in temperature (Oppelt, Patlak, Zubrod & Rall, 1964). Outside the meninx primitiva is the extrabrain fluid, EBF, which differs from VF. The EBF may be regarded as a large stagnant pool of plasma; exchanges between the blood and the EBF are very much slower than between the blood and the VF (Zubrod & Rall, 1959; Oppelt, Bunim & Rall, 1963). Zubrod & Rall (1959) suggest that the EBF is produced directly by the vessels of the endorachis, and serves as a mechanical buffer to the brain.

The extent of the space containing the EBF in the Port Jackson shark is shown in Fig. 1. The olfactory tracts and olfactory lobes are surrounded by a particularly extensive cavity. It is separated from the olfactory capsule by a fibrous membrane to which the leaflets of olfactory epithelium are attached. The internal and external nares are so arranged that respiration serves to carry a stream of water over the olfactory leaflets (Negus, 1958) and during a cough a portion of the water expelled flushes the leaflets and flows out from the external nares. The walls of the cranial cavity are elsewhere of dense cartilage, and the thin membranous boundary between the olfactory capsules and the cranial cavity would appear to be a likely place where respiratory pressures might be communicated to the extrabrain fluid.

Mean pressure of the EBF

The mean pressure of the EBF in nine Port Jackson sharks following at least 12 h of rest was 1.9 ± 1.4 cm H₂O. The pressure in a particular fish was maintained constant over the 3 to 4 days of the experiments; if one ml of EBF was aspirated the pressure would fall sharply and return to the preceding level. If 1 ml of elasmobranch saline was injected into the EBF its pressure would rise abruptly and return to the previous pressure with a time constant of 3 ± 0.3 min. During the course of experiments we sometimes noted a change of EBF to a new and higher level at which the mean pressure was maintained.

Pulsatile pressures in the EBF

The stable pressure of the EBF in resting fish was commonly disturbed by pulses; analysis showed that these had their origin in the change in orobranchial pressure due to respiration and coughing, and in the change of dorsal aortic blood pressure due to the normal pumping action of the heart. In Fig. 2 two sets of traces derived from the same fish demonstrate this. At EBF pressures below 2 cm H₂O respiratory pulsations were dominant; the small pressure pulsations caused by rhythmic coughing were similarly communicated in these circumstances. At higher EBF pressures above 5 cm H₂O the blood pressure pulse was impressed upon the EBF pressure trace. In Fig. 2 B the EBF pressure had spontaneously risen to 7–10 cm H₂O. Although the transient falls in blood pressure due to the natural cardiac arrhythmia (Satchell, 1968) were also transferred to the EBF, slow changes of pressure extending over several minutes were not and there was no significant correlation between mean blood pressure and mean EBF pressure calculated from all the fish used in the investigation.

The tendency for low EBF pressure to favour the appearance of respiratory pulsations in the EBF, and for higher EBF pressure to favour the appearance of blood

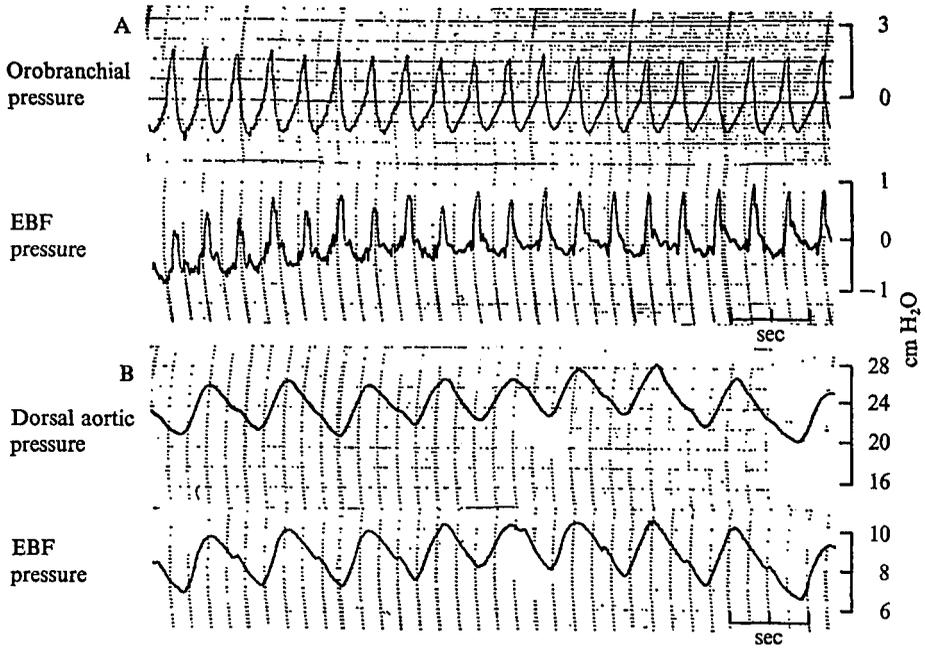


Fig. 2. Two E.B.F. pressure traces from the same fish showing change in pattern of pulsatile pressures with change of mean level of *EB.F.*



Fig. 3. Pressure trace from E.B.F. showing pulsations caused by normal respiration, cough, and blood pressure pulse.

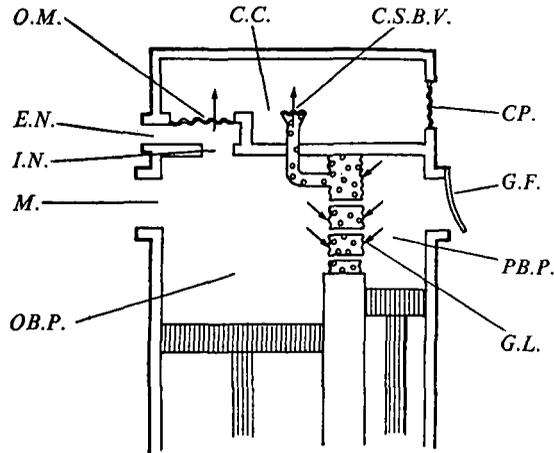


Fig. 4. Model showing postulated routes of communication of pharyngeal pressure pulses to EBF. Modified from Hughes & Ballintijn (1965). C.C. cranial cavity, CP. compliance of system, C.S.B.V. craniospinal blood vessels, E.N. external nares, G.F. gill flaps, G.L. gill lamellae, I.N. internal nares, M. mouth, OB.P. orobranchial pump, O.M. olfactory capsule membrane, PB.P. parabranchial pump.

pressure pulsations could be repeatedly demonstrated by deliberately withdrawing or adding fluid to the cranial cavity. In Fig. 3 a trace of complex form displays EBF pulses caused by respiration, rhythmic coughing and blood pressure. It was recorded in a fish with an intermediate level of EBF pressure (4–7 cm H₂O).

The mechanisms of transfer of pressure pulses

The anatomy of *Heterodontus* suggests that the cranial and spinal cavity are partly rigid and partly compliant. Fig. 4 presents a model of such a system. At low EBF pressures the cranial compliance, CP, would be unstretched but the large area of the olfactory capsule membrane would permit some transfer of the changes of pressure in the olfactory capsule, derived from the orobranchial cavity via the internal nares. It is known that the magnitude of the orobranchial respiratory pressure pulsations are small (1–2 cm H₂O) compared with the pulse pressure of the blood (7–10 cm H₂O). The failure of the blood pressure pulse to be transferred at low EBF pressure would be explained if the changes in the volume of the craniospinal blood vessels were small compared with the changes caused by the movements of the olfactory capsule membrane. At low EBF pressures the unstretched cranial compliance would accommodate the small volume change injected into the system by the dilation of the craniospinal vessels. This would result in little change in EBF pressure. Raised EBF pressure, however, would stretch the cranial compliance and enhance the transfer of the blood pressure pulse. The small volume changes caused by it would result in larger changes in EBF pressure.

The model (Fig. 4) also suggested how the two routes of transfer of orobranchial pressure pulses might separately be studied. The direct route through the olfactory capsular membrane was investigated by enclosing a pressure-recording cannula and an injection cannula into an olfactory capsule sealed off with dental plastic. The

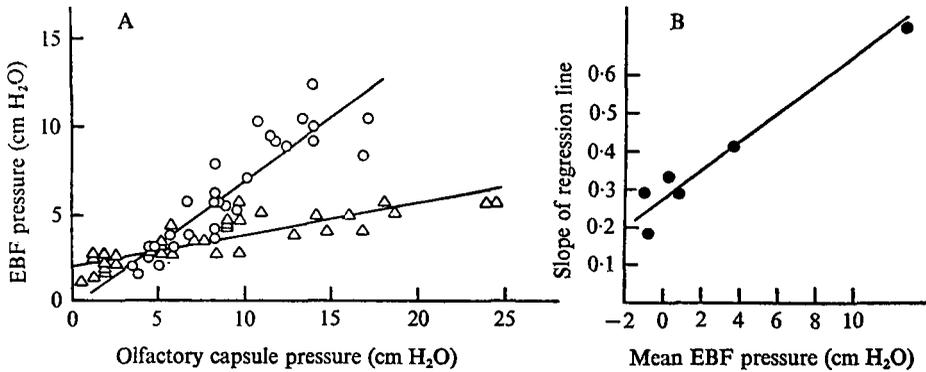


Fig. 5. A. Regression of amplitude of EBF. pressure pulse on amplitude of induced olfactory capsule pressure pulse at two levels of EBF. mean pressure. Δ , EBF. mean pressure = 2.5 ± 0.3 cm H₂O; equation = $Y = 0.19x + 2.0$, $S_{yx} = 1.4$, $P < 0.001$. O, EBF. mean pressure = 10.0 ± 1.0 cm H₂O; equation = $Y = 0.72x - 0.3$, $S_{yx} = 3.1$, $P < 0.001$.

B. The increase in the slope of the regression in 5 A, with increase of mean EBF. pressure. The results are derived from one fish. Equation = $Y = 0.035x + 0.29$. $S_{yx} = 0.05$, $P < 0.01$.

transfer of artificial pressure pulses created by injecting and withdrawing small volumes of fluid from the capsule could thus be examined with the knowledge that the branchial blood system was excluded. The indirect route, whereby orobranchial pressure pulses were transferred to the EBF through the intermediary of the blood system, was examined in two stages. Records of the amplitude of corresponding pressure pulses in the pharynx and the dorsal aorta, caused by coughs and respirations, enabled the first step of the transfer to be analysed. The considerable range of orobranchial pressures spanned by normal respirations and by rhythmic and evoked coughs provided material for a regression analysis. The second step, the transfer of dorsal aortic pressure pulses to the EBF, was examined by performing a regression analysis of the EBF pulse pressure on the normal dorsal aortic blood pressure pulse. This transfer does not include any pathway through the water within the pharynx, and thus enables this link to be analysed in isolation.

The direct transfer of orobranchial pressure to the EBF

The cavities of the olfactory capsules communicate with the orobranchial cavity through the wide internal nares and the drop of pressure between the two recording sites was too small to be measured during normal respiration and coughing; for purposes of analysis they have been regarded as equal.

When artificial pressure pulses were generated within the sealed olfactory capsule, a proportion of the pressure pulse appeared in the EBF record. Fig. 5A presents the results of one of three similar experiments. It can be seen that the slope of the regression line increased from 0.19 to 0.72 as the EBF mean pressure increased from 2.5 ± 0.3 to 10.0 ± 1.0 cm H₂O. In Fig. 5B the increase in slope with increase of EBF pressure is shown for another fish. From this graph we can infer that at the mean EBF pressure calculated from nine fish (1.9 ± 1.4 cm H₂O) approximately one-third of the orobranchial pressure would be transferred to the EBF via the olfactory capsule and that this fraction would increase with increase of EBF pressure.

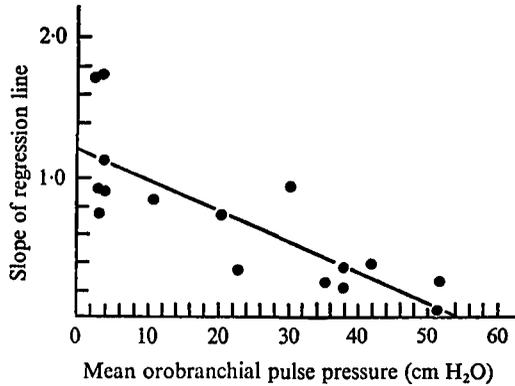


Fig. 6. The decrease of the slope of the regression of the amplitude of the dorsal aortic pressure pulse on the amplitude of the orobranchial pressure pulse as the latter increases. Equation = $Y = 1.21 - 0.022x$. $S_{yx} = 0.33$, $P < 0.001$.

The transfer of orobranchial pressure to the dorsal aorta

Regression analysis of the pressure pulse in the dorsal aorta, caused by a cough or respiration, on the amplitude of the corresponding pulse in the orobranchial cavity showed that the slope of the regression was independent of EBF pressure; this result was to be expected as the transfer depends only on the compression of branchial blood vessels by respiratory muscles. Small coughs of the type seen in rhythmically coughing fish (Fig. 3) showed a steeper slope than large coughs, i.e. they were more completely transferred to the dorsal aorta. The value of the slope of the regression line diminished as the mean amplitude of the population of coughs analysed increased. In Fig. 6 the value of the slope is plotted against the mean amplitude of 16 populations of coughs derived from six fish. The five smaller ones were from periods when the fish were coughing rhythmically. The eleven larger ones were groups of evoked coughs. The graph reveals that coughs above 52 cm of water did not generate pulses of any greater amplitude in the dorsal aorta. This suggests that the muscular contractions that generate these stronger coughs emptied and perhaps temporarily obliterated the blood vessels close to them. Small rhythmic coughs show a slope greater than 1; the mean slope for five fish was 1.25 ± 0.42 . A possible explanation of this is that some part of the branchial vasculature is so placed in relation to respiratory muscles that when they contract they generate a greater pressure on the adjacent blood vessels than they do on the water within the orobranchial cavity. The septal constrictor muscles, which effect a vertical compression of the gill septa, are known to be active in both spontaneous and evoked coughs (Satchell & Maddalena, 1972) and would be well situated to compress the smaller afferent and efferent arterioles to and from the gill lamellae.

There is evidence that the effectiveness of the transfer of orobranchial pressure to the dorsal aorta varies with the position of the cough within the cardiac cycle. In one fish with minimal cardio-respiratory coupling rhythmic coughs of equal amplitude occurred; sufficient trace was run to enable populations of coughs to be analysed from four segments of the cardiac cycle, i.e., systole, up to the peak of the dorsal aortic blood-pressure pulse, and three equal periods termed early, mid and late diastole. Coughs of equal amplitude occurring in systole evoked a dorsal aortic pressure pulse

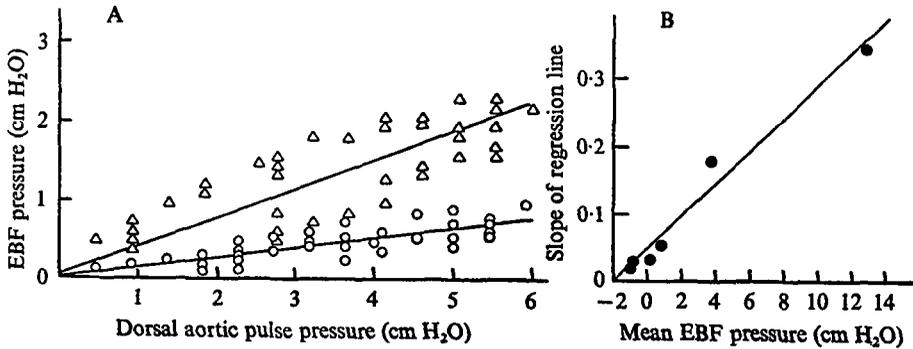


Fig. 7. A. Regression of amplitude of EBF pulse pressure on pulse pressure in the dorsal aorta. O, EBF mean pressure = 3 ± 0.5 cm H₂O. Equation = $Y = 0.13x$. $S_{yx} = 0.39$, $P < 0.001$. Δ, EBF mean pressure = 14.0 ± 0.3 cm H₂O. Equation = $Y = 0.38x + 0.03$, $S_{yx} = 0.87$, $P < 0.001$.

B. The increase in the slope of the regression in 7 A, with increase of mean EBF pressure. The results are derived from one fish. Equation = $Y = 0.024x + 0.049$, $S_{yx} = 0.026$, $P < 0.001$.

which was 20% greater than that evoked in late diastole; the results were significant at the 1% level. The dilation of the branchial vessels by the blood ejected into them at systole permitted, we may suppose, a greater volume of blood to be forced into the dorsal aorta by the compression of the vessels by the cough.

The transfer of dorsal aortic pressure to the EBF

The cranial vessels all arise as branches from the internal carotid arteries and these vessels in turn take origin from the dorsal aorta; the segmental arteries of the spinal cord similarly arise from the dorsal aorta. The effectiveness of transfer of the dorsal aortic pressure pulse to the EBF at different levels of mean EBF pressure was analysed. Fig. 7A displays the results from one of four similar experiments. It can be seen that the slope changes from 0.13 at 3 ± 0.5 cm H₂O to 0.38 at 14 ± 0.3 cm H₂O. Fig. 7B shows the increase of slope of this regression line with increasing EBF mean pressure; the results are derived from one fish. A similar curve was derived from pooled results from four fish. Approximately one-eighth of the normal dorsal aortic blood pressure pulse was transferred to the cranial fluids at normal levels of EBF pressure.

The results thus show that whether pressure pulses were delivered to the cranial fluids by pressures external to the olfactory membrane (Fig. 5B), or were injected into the cranial cavity through the medium of the craniospinal blood vessels (Fig. 7B), transfer was increased when the level of EBF pressure was raised. In both situations the stretching of the compliance in the craniospinal canal altered the volume-elasticity ratio of its walls and favoured transfer.

The overall effectiveness with which cough pressure pulses in the orobranchial cavity were transferred to the EBF via the indirect route was calculated as the product of the separate values for the transfer from the orobranchial cavity to the dorsal aorta, and from the dorsal aorta to the EBF. At normal EBF pressure this would give a value of 0.16 for small rhythmic coughs, i.e. 1.25×0.13 . An increase of the mean level of

EBF pressure will increase transfer by favouring the second link; at 14 cm H₂O it would have a value of 0.47.

The slope of the regression of EBF cough pressure on orobranchial cough pressure in individual fish likewise increased with increase of mean EBF pressure. In one fish showing rhythmic coughing an increase of EBF pressure from 2.5 ± 1.5 to 8 ± 2.0 cm H₂O increased the slope from 0.22 to 0.52 ($P < 0.01$). This, however, must reflect both the increased transfer directly across the olfactory capsule and also the increased transfer from the cranial blood vessel to the EBF. There is no direct way to separate the two contributions which jointly elevate EBF pressure in the situation of the spontaneous or evoked cough.

DISCUSSION

Hamilton *et al.* (1936, 1954) argued that in man the craniospinal cavity should be regarded as a functional extension of the thoracic cavity. The normal systolic rise in blood pressure causes a rise of intraspinal pressure of only 1–2 mmHg, whereas a cough causes a rise as great as or even greater than the rise it causes in the arteries. They suggested that the rise in thoracic pressure is communicated to the spinal canal by (a) the inward movement of the spinal nerves and the loose areolar tissue that surrounds them, (b) the cerebrospinal fluid from under the invaginations of the dura around the nerves, and (c) of venous blood from the paravertebral plexuses. They showed that the rise in pressure of the cerebrospinal fluid offset the rise of blood pressure in the craniospinal blood vessels and protected them from sudden net increases in transmural pressure.

In the Port Jackson shark pressure pulses in the pharynx caused by coughing similarly transmit a pressure pulse to the dorsal aorta. During a cough the normal gradient of pressure across the gill lamellae is reversed; pressure in the parabronchial cavity rises above that in the orobranchial cavity and brings about a back-flush of the fine channels of the gills (Satchell & Maddalena, 1972). It has been suggested in this paper that during the contraction of the parabronchial cavities the septal constrictor muscles squeeze the small afferent and efferent branchial arterioles.

Rhythmic coughs generated low orobranchial pressures within the range of 2–8 cm H₂O. Let us consider the magnitude of the dorsal aortic and EBF pressure pulses derived from a cough causing an orobranchial pressure of 8 cm H₂O. It will be transferred to the dorsal aorta with little or no loss; approximately one-eighth of this dorsal aortic pulse will be transferred to the EBF at normal levels of EBF mean pressure. But approximately one-third of the orobranchial pulse will be directly transferred through the olfactory capsule membrane; thus the 1 cm H₂O rise in pressure in the cranial vessels will be offset by a counter rise in pressure of 2.7 cm H₂O in the EBF. Here as in mammals the magnitude of the directly communicated pulse exceeds that transferred via the blood system.

The pressures transferred to the EBF by rhythmic coughs were very small, but there are reasons to suppose that greater pressures occurred in other circumstances. Increase of the EBF mean pressure to 10 cm H₂O more than doubled the transfer of the pressure pulse from the arteries to the cranial fluids; such pressure was observed to occur in the laboratory in apparently healthy fish. The observation that the transfer

of the orobranchial pressure pulse to the blood system was greater during the ejection phase of systole suggests that the increased blood pressure which accompanies exercise in fish may enhance the overall communication of the cough impulse to the brain. Spontaneous and evoked coughs exceeding 70 cm H₂O have been recorded in the laboratory and larger coughs may occur in nature.

The functional similarity in the mechanism outlined in this paper between a fish and a mammal is the more remarkable because the direct communication of the cough pressure is by a totally different route. In the air-breathing mammal the cranial cavity is largely separated from the olfactory chamber by the bony cribriform plate; the rise of thoracic pressure that accompanies a cough is largely released through the mouth. The cough pressure is communicated from the thorax to the craniospinal canal. In fish the great importance of the olfactory sense has necessitated an extensive area of olfactory epithelium thinly separated from the related olfactory lobes of the brain, and it is through this route that the cough pressure is directly transferred to the cranial fluids. Hamilton *et al.* (1936) suggest that in mammals this mechanism serves to protect the delicate cranial vessels from rupture during coughing. In man, veins in the nose, conjunctiva and anus, which lack this protective counter pressure, sometimes burst during prolonged paroxysms of coughing (Sharpey-Schafer, 1953). Mechanical displacement of masses of neurones may be harmful to their integrative functions. Kerr & Eich (1961) and McIntosh *et al.* (1956) suggest that in man cough syncope, the fainting which sometimes accompanies even a single cough, may involve a concussive event in which cortical neurones are depolarized by the mechanical shock derived from the cough. Whether such hazards attend coughing in fish is of course conjectural; it is of interest that a similar protective mechanism operates in such a different anatomical situation.

SUMMARY

1. The mean pressure of the extrabrain fluid (EBF) of nine Port Jackson sharks (*Heterodontus portusjacksoni*) following 12 h rest was 1.9 ± 1.4 cm H₂O.
2. Low to normal EBF pressures favoured the appearance of respiratory pressure pulsations in the EBF; higher pressures favoured the appearance of blood pressure pulsations.
3. Two routes of communication of pressure pulses from the orobranchial cavity were investigated by regression analysis of pulse pressure records;
 - (a) a direct route from the olfactory capsule to the cranial cavity
 - (b) an indirect route via the branchial blood vessels and the craniospinal vessels.
4. The hypothesis is advanced that a protective mechanism exists, paralleling that in mammals, whereby dilation of craniospinal vessels during coughing is offset by the directly communicated pressure pulse in the extrabrain fluid.

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