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MAYER WAVES IN THE CIRCULATION OF A TELEOST FISH

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ABSTRACT Regular oscillations in arterial blood pressures identical to mammalian Mayer waves were recorded in unanaestetized trout (Salmo gairdneri). The waves were associated with hemorrhage, were caused by fluctuations in systemic vascular resistance, and were sometimes accompanied by fluctuations in cardiac output of opposite phase. Alpha-adrenergic blockade eliminated the phenomena; muscarinic cholinergic blockade was ineffective. The existence of Mayer waves provides evidence for a nervous control of vasomotor tone in teleosts.

Although innervation of the blood vessels in fish has been extensively documented by histological techniques, there exists no evidence that the autonomic nervous system controls vascular resistance in vivo (Campbell, '70). On the contrary, the limited data available suggest that circulatory catecholamines maintain vasomotor tone (Randall and Stevens, '67; Campbell, '70). I now report the occurrence in Salmo gairdneri of phenomena apparently identical to the Mayer vasomotor waves of mammals. Mayer waves are known to be mediated through the effect of a phasic sympathetic outflow on systemic vascular resistance (Guyton and Harris, '51; Ferretti et al., '65; Kaminski et al., '70).

MATERIALS AND METHODS Sixty-nine freshwater rainbow trout (100-725 g), acclimated to 14.5 ± 1.5^{o} C for at least 1 week, were anaesthetized in MS - 222 (1:15000). Cannulae were implanted in the buccal cavity, ventral aorta, dorsal aorta, caudal artery, caudal vein, and subintestinal vein (Holeton and Randall, '67; Wood and Randall, '71). Electro-magnetic flow probes (Biotronex) were placed around the ventral aorta for direct determination of cardiac output. All fish were fitted with buccal, dorsal aorta, and subintestinal vein cannulae; the other catheters and the probe were added in various combinations. The operative procedures were severe and the trout suffered variable blood loss. The animals were then placed on a peg-board restraint inside a darkened Perspex box and allowed to recover for at least 6 hours. Data were taken up to 6 days post-operatively. Blood pressures and flows were monitored by standard methods and displayed on a Sanborn 6 channel recorder. True flow probe zero was determined periodically by briefly stopping the heart with acetylcholine chloride (1-10 nM/100 g) injected into the subintestinal vein. A record of instantaneous heart rate was obtained by triggering a linear output ratemeter from a blood pressure or flow signal.

RESULTS Spontaneous, regular fluctuations in dorsal aortic blood pressure were observed in 27 of the trout (fig. 1). These waves were approximately sinusoidal in shape with an amplitude ($\bar{x}$ ± S.E.) of 4.7 ± 0.4 cm H_2O (range 1.5-12.5) and period of 31.7 ± 1.8 sec (range: 13.8-49.8), and occurred in waxing, sustained, and waning forms. These events were in no way associated with ventilation as measured by the buccal pressure (figs. 1b, c, d) and thus would appear to be Mayer rather than Traube-Hering waves (Schweitzer, '45). However, much faster respiratory waves in blood pressures, cardiac output, and heart rate were commonly seen, sometimes on the same record as the Mayer waves (figs. 1a, c, d). These probably result from direct mechanical effects of the breathing pump.

The Mayer waves were always synchronous and of similar size in the dorsal aorta and caudal artery (fig. 1b). Such oscillations were never seen in the non-pulsatile venous pressure, as recorded from the caudal vein (1) (figs. 1a, d). Of particular importance was the finding that the ventral aortic pressure always exhibited oscillations of approximately equal size and perfect phase and synchrony with the dorsal aortic waves (fig. 1a). In view of the direct serial arrangement of the two major vascular beds (gills and body) in the teleost, these observations must mean that the waves arose in the most part from fluctuations in systemic, rather than branchial, vascular resistance, provided that flow variations were not the cause. Cardiac output determinations confirmed this point. Of the 7 animals in which successful flow measurements were obtained during Mayer waves, the mean cardiac output remained constant in 4 fish (fig. 1c) and showed slight oscillations of opposite phase to the systemic pressure fluctuations in the other 3 (fig. 1d). These variations represented stroke volume alterations; heart rate changes, other than those associated with ventilation, were never seen. After atropinization to block vagal tone, elevated systemic resistance caused by adrenaline injections also decreased cardiac output through an apparently identical passive mechanism (Wood, unpublished). Thus the situation in the trout appears identical to that in the anaesthetized dog, where aortic flow varied in opposition to pressure during Mayer waves due to oscillations in systemic vascular resistance (Killip, '62).

The competitive α-adrenergic (yohimbine hydrochloride; 100 nM/100 g), muscarinic cholinergic (atropine sulfate; 100 nM/100 g), and ganglionic (hexamethonium bromide; 1 μM/100 g) antagonists were administered via the subintestinal vein during Mayer waves. By the criterion adopted (2), yohimbine blocked the waves in 9 out of 9 fish; atropine was ineffective in 8 out of 9 fish. Thus α-adrenergic receptors, which predominate in the systemic vasculature (Wood, unpublished), are involved in the genesis of the waves. Results with hexamethonium in 5 out of 5 fish were equivocal; although there was an initial blockage coincident with a depressor effect, the waves tended to reappear with much longer periods (>60 sec) after 20-60 min (3).

The trout in which Mayer waves occurred spontaneously were characterized

TABLE 1

Cardiovascular and respiratory parameters in S. gairdneri

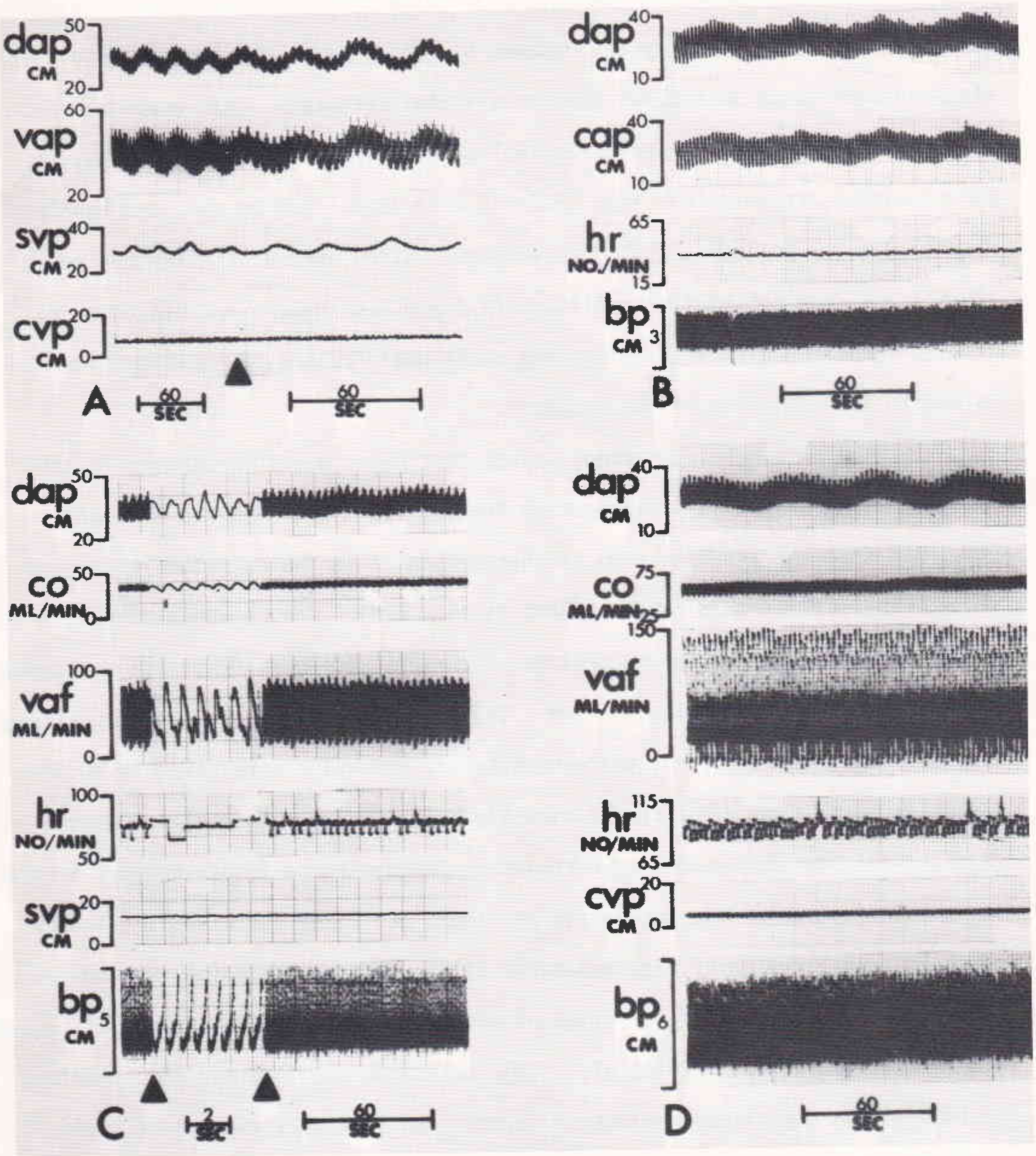
Parameter	No Waves	Waves	p
Ventral aortic pressure ($cm\ H_2O$)	43.5 ± 2.7 (12)	36.6 ± 3.1 (7)	n.s.
Dorsal aortic pressure ($cm\ H_2O$)	35.3 ± 1.0 (49)	29.5 ± 1.2 (27)	<0.001
Caudal artery pressure ($cm\ H_2O$)	34.3 ± 1.7 (15)	27.2 ± 1.7 (7)	0.02
Caudal vein pressure ($cm\ H_2O$)	5.4 ± 0.4 (18)	5.9 ± 0.6 (11)	n.s.
Heart rate (beats/min)	76.8 ± 1.6 (52)	82.9 ± 2.3 (27)	<0.05
Cardiac output (ml/kg/min)	34.04 ± 3.76 (13)	43.74 ± 7.30 (7)	n.s.
Cardiac stroke volume (ml/kg/beat)	0.449 ± 0.050 (13)	0.542 ± 0.088 (7)	n.s.
Ventilation rate (breaths/min)	90.6 ± 1.4 (44)	102.7 ± 2.6 (24)	<0.001
Buccal pressure amplitude ($cm\ H_2O$)	1.87 ± 0.11 (45)	2.80 ± 0.24 (24)	<0.001
Hematocrit (%)	17.1 ± 1.2 (27)	10.8 ± 1.8 (13)	<0.01

Note: where waves were not seen on the first post-operative day, but appeared on a subsequent day, single entries were made in both categories. Means ± 1S.E. (N). Blood pressures are expressed as area means.

by significant elevations of heart rate and breathing rate and amplitude (table 1), differences which probably reflected stress. That this stress may have been due to blood loss was indicated by the significant depressions of systemic pressures

FIGURE LEGENDS

1 Original recordings from 4 trout during spontaneous Mayer waves.
dap = dorsal aortic pressure; vap = ventral aortic pressure;
cap = caudal artery pressure; svp = subintestinal vein pressure;
cvp = caudal vein pressure; bp = buccal pressure;
hr = instantaneous heart rate; vaf = ventral aortic flow;
co = mean cardiac output, obtained by electronic averaging of vaf.
Arrows denote changes in recorder speed. (A) 304 g. (B) 176 g. (C) 543 g. Note the ventilatory interaction on dap, vaf, and hr traces causing respiratory waves. Note also the constancy of co during Mayer waves. (D) 718 g. Note slight fluctuations in co of opposite phase to Mayer waves in dap.


dap CM 50 20
vap CM 60 20
svp CM 40 20
cvp CM 20 0
A
60 SEC
60 SEC
dap CM 40 10
cap CM 40 10
hr NO./MIN 65 15
bp CM 3
B
60 SEC
dap CM 50 20
co ML/MIN 50 0
vaf ML/MIN 100 0
hr NO/MIN 100 50
svp CM 20 0
bp5 CM
C
2 SEC
60 SEC
dap CM 40 10
co ML/MIN 75 25
vaf ML/MIN 150 0
hr NO/MIN 115 65
cvp CM 20 0
bp6 CM
D
60 SEC

and hematocrit (table 1); hemorrhagic hypotension is a common cause of Mayer waves in mammals (Guyton and Harris, '51). Nine trout originally exhibiting no waves were experimentally hemorrhaged by 0.5% body weight (approximately 10% blood volume) every 30 minutes from an arterial catheter. This procedure was successful in producing Mayer waves in 7 of the fish after 1-5 bleedings, as dorsal aortic pressure fell from 36.3 ± 2.7 to 30.3 ± 2.8 cm H_2O, and hematocrit from 17.3 ± 2.2 to 11.6 ± 2.4%. These oscillations were of similar period (29.4 ± 2.4 sec) but smaller amplitude (2.0 ± 0.1 cm H_2O; $p < 0.01$) to those arising spontaneously, indicating that additional factors may have been involved in the causation of the latter.

DISCUSSION General agreement exists that Mayer waves in mammals reflect the abnormal oscillation of a negative feedback control for blood pressure or flow, and that the efferent limb of this mechanism is the sympathetic nervous system (Ferretti et al., '65; Kaminski et al., '70). The presence of such waves in the rainbow trout therefore provides the first strong evidence for a nervous regulation of vasomotor tone in vivo. The abolition of the waves by α-adrenergic blockade supports this view; the α-receptor is generally considered to be the adreno-receptor type which can be directly activated by sympathetic innervation (Ross, '71). An involvement of circulatory catecholamine levels appears highly improbable in view of the regularity and short period of the waves and the apparently long lifetime of catecholamines in the trout circulation (Nakano and Tomlinson, '67). A variety of afferent pathways for the negative feedback system have been invoked (Kaminski et al., '70), but chemoreceptors and baroreceptors would seem the most likely points of input. The lack of variation in heart rate during Mayer waves in the trout, as in mammals (Killip, '62), may indicate a minimal role for baroreceptors, for they normally mediate a negative chronotropism in response to rather small systemic pressor events (Wood, unpublished).

The pseudobranch, which has recently been shown to possess both chemoreceptor and baroreceptor capabilities (Laurent and Rouzeau, '72), may be suggested as the possible afferent limb of the system in the trout.

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1 Large fluctuations (5-40 cm H_2O) often appeared in subintestinal vein pressure of superficial similarity to the systemic waves (fig. 1a), but were never correlated with the Mayer waves, and frequently occurred in their absence. Operating table observations showed that they simply reflected spontaneous intestinal motility.

2 All three agents caused depressor effects which by themselves were capable of temporarily eliminating the waves. Thus the criterion applied was whether the waves reappeared over the following two hours, a period during which yohimbine and atropine were known to remain effective against injected agonists.

3 However this time may correspond to the period of effectiveness of hexamethonium in the trout, if the latter can be deduced from the drug's non-specific action in inhibiting ventilation.