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SHORT COMMUNICATION

DEPENDENCE OF BLOOD VISCOSITY ON HAEMATOCRIT AND SHEAR RATE IN A PRIMITIVE VERTEBRATE

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Hagfish have an unusual circulation with intravascular pressures that are lower than those in other vertebrates (Davie *et al.* 1987; Forster, 1989) and since peripheral resistances appear similar to those of teleost fishes (Flood, 1979; Elger, 1987), it follows that blood flow rates will also be lower. One might therefore predict that the relatively low haematocrits in hagfish (Johansen *et al.* 1962; Forster *et al.* 1989) and lack of plasma albumins (Manwell, 1963) would maintain a relatively low blood viscosity at low flow rates when blood tends to become more viscous by virtue of its non-Newtonian behaviour (McDonald, 1974; Fletcher & Haedrich, 1987).

Viscosity measurements were made on the blood and plasma of the hagfish, *Eptatretus cirrhatus* (Forster), to determine whether blood viscosity was unusually low in a vertebrate with a circulation operating at low shear rates, and to see whether this primitive vertebrate conformed to optimal haematocrit theory (cf. Crowell & Smith, 1967).

Hagfish were cannulated *via* the ventral aorta, and maintained in running sea water. Heparinized whole blood was drawn for measurements of viscosity, haematological parameters and total plasma protein (Biuret reaction). Packed erythrocytes were resuspended in autologous plasma to provide a series of haematocrits (Hct) from 0 to 40 %.

The viscosity of 0·5 ml samples was measured at 20 °C in a rotating cone-plate viscometer (model LVTD, Brookfield Engineering, Stoughton, MA) equipped with cone angle of 0·8° (Fig. 1).

Haematological data are summarized in Table 1. The linear dimensions for hagfish erythrocytes were about twice those reported for teleost fishes (e.g. Hughes *et al.* 1982; Hughes & Kikuchi, 1984). A comparison of vertebrate erythrocytes with widely differing sizes led Chien *et al.* (1971) to the conclusion that erythrocyte volume was not an important determinant of blood viscosity. The mean ventral aortic Hct value reported here of 12·6 % is low among vertebrates. Total plasma protein in the hagfish was about half that recorded for teleosts (Graham & Fletcher, 1985), no doubt because of the absence of albumin.

Key words: blood, viscosity, haematocrit, hagfish, *Eptatretus cirrhatus*.

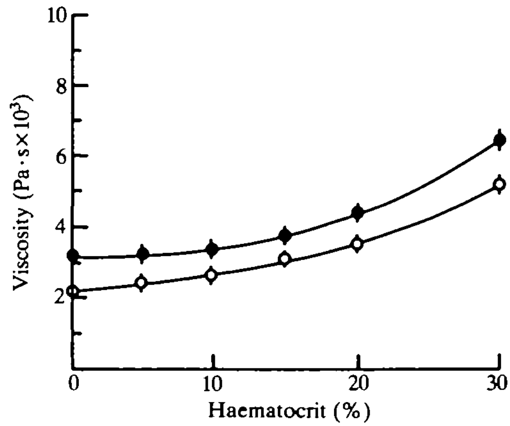

Fig. 1. Viscosity of hagfish blood as a function of haematocrit at shear rates of $225\,s^{-1}$ (○) and $45\,s^{-1}$ (●). Mean values ± s.e.m. ($N = 4$).

Table 1. *Haematological parameters from ventral aortic blood of hagfish*

Haematocrit (%)	12·6 ± 0·4
White blood cells (%)	3·3 ± 0·4
No. of red cells per μl $\times 10^{-6}$	0·223 ± 0·006
Mean cell volume (fl)	538·3 ± 43·3
Haemoglobin	
(g%)	3·04 ± 0·13
(mmol l^{-1})	0·47 ± 0·02
Mean cell haemoglobin content	
(g%)	24·2 ± 1·2
(mmol l^{-1})	3·71 ± 0·18
Red blood cells	
Length (μm)	19·8 ± 0·15
Breadth (μm)	13·9 ± 0·21
White blood cells	
Length (μm)	22·4 ± 0·38
Breadth (μm)	17·2 ± 0·22
Total plasma protein (g%)	2·38 ± 0·40
Viscosity $45\,s^{-1}$ (Pa·s×10³)	3·74 ± 1·01
Viscosity $90\,s^{-1}$ (Pa·s×10³)	2·89 ± 0·54
Viscosity $450\,s^{-1}$ (Pa·s×10³)	2·47 ± 0·28

Values are means ± s.e.m. for $N = 7$.

Non-Newtonian behaviour of hagfish erythrocytes was shown by the marked rise in viscosity at low shear rates (equivalent to flow). The magnitude of shear dependence is quantified by the viscosity ratio $(\eta_L - \eta_H)\eta_H$ (Table 2), where η_L and η_H are the viscosities (in Pa·s $\times 10^{-3}$) at shear rates of 4·5 and $90\,s^{-1}$, respectively (after Fletcher & Haedrich, 1987). Shear dependence is not signifi-

Table 2. *Shear dependence of hagfish blood viscosity (4·5 to 90 s^{-1}) related to haematocrit (20°C)*

	Haematocrit (%) 0	5	10	15	20	30
$(\eta_{4\cdot5}-\eta_{90})/\eta_{90}$	2·19 ± 0·21	2·36 ± 0·36	2·26 ± 0·31	2·67 ± 0·41	1·37 ± 0·19	0·57 ± 0·10

Values are means ± S.E.M. ($N=4$).

cantly different between 0 and 15 % Hct, but becomes significantly less ($P<0{\cdot}01$) at higher Hct.

Our measurements on blood viscosity are the first to be reported from cannulated fish. High viscosities arising from elevated haematocrit will result from handling and sampling stresses. Comparison with other viscosity measurements is therefore of limited value. Nevertheless, at the lowest shear rates, blood viscosity in the hagfish is less than that of the winter flounder (at 0°C), similar to that in shorthorn sculpin and arctic char (at 0°C), but greater than that of the rainbow trout (at 15°C) (Graham & Fletcher, 1985; Graham *et al.* 1985; Fletcher & Haedrich, 1987). For winter flounder at the warmer summer temperatures prevailing in the south of its distribution range, blood viscosity is approximately 30×10^{-3} Pa·s (Graham & Fletcher, 1983).

Hagfish blood, because of its low haematocrit, which is further reduced in the subcutaneous sinus, has a low viscosity; thus, the cardinal and caudal hearts returning the subcutaneous sinus blood to the central circulation will have to exert less force. This might be seen as a fortuitous advantage of the plasma-skimming occurring at the point of entry of the sinus blood (Forster *et al.* 1989).

The measurements of viscosity as a function of haematocrit provided the

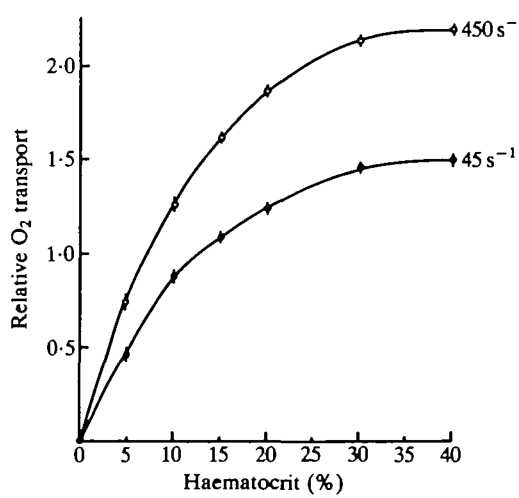

Fig. 2. Optimal haematocrit curves for hagfish blood at shear rates at 450 s^{-1} (O) and 45 s^{-1} (●). Mean values ± S.E.M. ($N=4$).

opportunity to test optimal haematocrit theory in a primitive vertebrate. The maximum value of oxygen transported as a function of haematocrit can be determined *in vitro* (Crowell & Smith, 1967) and for a number of vertebrates it has been shown that the predicted haematocrit is often identical with the observed haematocrit *in vivo* (Stone *et al.* 1968; Snyder, 1971; Weathers, 1976). Since it has been shown that oxygen transport is proportional to blood oxygen capacity divided by resistance to flow (see Snyder, 1983), oxygen transport capacity (OTC) can be calculated using the measured values of haemoglobin concentration, [Hb], and blood viscosity using the relationship: $OTC = 1{\cdot}3[Hb]/\eta$, where 1·3 is the volume of O_2 bound per gram of Hb, and η is viscosity in $Pa \cdot s \times 10^{-3}$ (Hedrick *et al.* 1986). The relative oxygen transport capabilities of hagfish blood at two shear rates are shown in Fig. 2. Clearly, haematocrit in the ventral aorta is such that only half the oxygen transport potential is realized. The significant consequence is a low resistance to blood flow. Speculation concerning the low haematocrit in hagfish must await further physiological measurements and, in particular, estimates of peripheral resistance and distribution of erythrocytes in the circulation.

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