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REGULAR ARTICLE

Towards a basic understanding of the properties of camel blood in response to exercise

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Abstract

The objective of the study was to investigate changes in blood fluidity in camels in response to exercise. 11 camels (9 male, 2 female) performed a 30 minutes run. Blood lactate changes indicated mild aerobic exercise. HCT and PCV remained essentially unchanged while plasma protein concentration decreased mildly suggesting a gain in blood volume of 1-2 L. Whole blood viscosity (WBV) did not change significantly at any shear rate (flow curves at logarithmic shear rate (SR) ramp, 37°C:11.6-500 s^{-1}), and viscosity ratio (WBV_{500s}^{-1}/ $WBV_{11.6s}^{-1}$) was maintained as well. RBC aggregation indices M0 and M1 did not change significantly either. The theoretical optimal HCT, i.e. the range of the HCT at which the O_2-transport capacity (HCT/WBV) is highest, was estimated by measuring WBV of RBC dilutions in autologous plasma. The RBC concentrations were measured as PCV and thus PCV/WBV plotted against PCV (2nd degree polynom). At 11.6 s^{-1} the "optimal HCT" was at a PCV of 49.2%, and decreased to 34.8% at 500 s^{-1}. In arteries and arterioles (high SR), the actual PCV observed may be regarded "optimal", whereas in venules and veins (low SR), the actual PCV observed was lower than its theoretical "optimal" value. This indicates that a possible increase in PCV might provide a sizable reserve in performance capacity. During a more strenuous exercise or at arid environments this would optimize O_2 transport at low shear areas by eventually preventing blood from becoming sluggish.

Key words: Blood viscosity, Camel, Exercise, Hemorheology, Optimal hematocrit

Introduction

Blood fluidity in athletes such as man, greyhounds and racehorses typically changes as a result of increasing hematocrit (HCT) in an effort to optimize oxygen delivery to the skeletal muscles. In the camel, however, there is no such extensive rise in HCT during exercise, yet camels are enduring performers over long distances and show remarkable race performances as well (Maloiy et al., 2009; Sharp, 2012).

The oxygen supply to the target organs basically depends on cardiac output and circulating blood volume, the geometries in the microvasculature, the diffusion distance between hemoglobin and myoglobin, and the amount of circulating red blood cells (RBC) and their oxygen content. The quantitative and qualitative properties of RBC together with the plasma fluidity combine to result in the fluidity of whole blood. The number and the size of RBCs are the determining factors for the hemoglobin carrying capacity. The qualitative properties include the RBC shape, the fluidity of the RBC cytoplasm, and the composite properties of the RBC membrane. These three main factors determine the ability of the RBC to deform and aggregate in relation to the actual shear stresses in the vasculature (Cokelet and Meiselman, 2007; Cooke and Lim, 2007; Baskurt, 2007; Lipowsky, 2007).

RBC deformability is basically determined by the cytoskeleton architecture and the intrinsic membrane fluidity of the phospholipid bilayer. In mammals, these two factors are highly species-specific (Nikinmaa, 1990; Windberger and Baskurt, 2007) and RBC generally present as biconcave discs. The RBC of camelids is exceptional among mammals as they appear as elliptical discs without the typical central depression (Smith et al., 1997; van Houten et al., 1992; Yamaguchi et al., 1987). Parts of a marginal band - which is usually present

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only in nucleated RBC – are found in the RBC cytoplasm of camelids (Cohan and Terwilliger, 1979), which may contribute to the specific shape of camelid RBC. This likely contributes to the low flexibility observed. Cell membrane folding and alignment in the flow field may also be altered as a result (Gaehtgens et al., 1981a; Gaehtgens et al., 1981b). As RBCs require parallel contact surfaces to aggregate, these properties could also prevent camelid RBC from developing extensive Rouleaux formation usually observed in other mammals.

The importance of RBC flexibility and aggregability is emphasized by their direct impact on tissue perfusion. RBC flexibility permits the capillary perfusion and determines oxygen transport within the microvasculature (Busse, 1997). The effect of RBC aggregability on tissue perfusion is more complex. Firstly, RBC aggregation occurs only at low shear rates ($<10\ s^{-1}$) typically present in venules and veins. At higher shear rates ($>20\ s^{-1}$) disaggregation of RBC-clusters takes place and at even higher shear rates RBC are then individually suspended in the plasma. This indicates that the presence of RBC aggregates depends on the level of the intravascular shear forces. Secondly, RBC aggregation is directly linked to the extent of the phase separation in arterial vessels. The majority of RBC is then located in a central column of the blood stream and lined by a marginal cell-free layer towards the vessel wall (Kim et al., 2009, Ong et al., 2012). This presents an efficient way of transporting RBC through arteries and arterioles by forming a "gliding layer". For the phase separation to occur, the blood cells and aggregates need to reach a critical size in relation to the vessel diameter. A cell-free layer is then formed between the corpuscular column and the vessel wall, which is responsible for the reduction of HCT in the microvascular system (the Fahraeus effect; Fahraeus, 1958). The width of this cell-free layer regulates the endothelial shear forces on endothelial cells, which in turn can moderate the vessel diameter through the release of vasoactive substances (Baskurt et al., 2004; Malek and Izumo, 1992; Moncada et al., 1991; Yalcin et al., 2008).

The above mentioned aspects demonstrate that blood possesses various mechanisms to adapt to changes in the vasculature such as geometry and intravascular pressure, and to moderate the distribution of RBC into the tissues. It is doubtful if the same mechanisms are also present in the camel, since camel RBC flexibility is very low and RBC aggregation is yet to be recorded. Given the particular morphology of camel RBC, and the absence of a rise in HCT during exercise in camels, we wondered what other factors are at play and how they change in response to exercise.

One possibility to describe the hemorheological status is the estimation of a so-called theoretical "optimal HCT" (Bogar et al., 2005; Hedrick et al., 1986; Nemeth et al., 2009). This value indicates the HCT at which oxygen transport capacity, measured by the ratio of HCT and blood viscosity, is at a maximum. It has to be kept in mind that the actual oxygen delivery may differ as factors such as O_2-affinity and -dissociation, or RBC transit time in the microvasculature (Cokelet and Meiselman, 2007) are not accounted for, and neither are hemodynamic parameters or vascular geometries. RBC transit time may be different in camels due to the specific RBC morphology. However, following the definition where "the maximum of this curve indicates a theoretical value indicating a range where the benefit of RBC in the bloodstream is not reversed by a concomitant increase of viscosity" (Nemeth et al., 2009), the estimation of this value still seems to be a very useful indicator.

The hemorheological status can also be described by flow curves where increasing shear rates are applied and the resulting changes in viscosity are measured by a rheometer. Flow curves are useful to show not only the blood viscosity at various shear rates, but also the degree of shear thinning as a function of build-up and degradation of structures within the sample. If blood has low RBC aggregation and low RBC flexibility, shear thinning is reduced.

To complete the description of the blood properties, RBC aggregation was measured.

Materials and Methods

Animals

Blood was collected from nine male and two female Arabian Camels (*Camelus dromedarius*) aged between 4 to 15 years, kept at the Kaalfontein Farm, Krugersdorp, Gauteng, Republic of South Africa. The animals were kept on a pasture with ad-lib access to grazing and water. Ethics committee approval was obtained from the University of Pretoria Animal Use and Care Committee (approval No. H007/09). The animals were clinically healthy at the time of the study with no reported disease or adverse observations during the six months prior to the study.

Experimental protocol

The study was conducted in the rainy summer season at 1700 m above sea level. Due to practical reasons the experiments were performed in three blocks of three and four animals respectively within a two week period. A four km warm-up (20 minutes) was followed by an eight km (25 minutes)

run on a level tar road. Blood was withdrawn from the jugular vein by a 20 mL syringe mounted with an 18 G needle just prior to and immediately after exercise, as well as after 30 minutes cool down period. Blood was transferred into sodium EDTA, sodium fluoride and sodium heparin tubes, placed on ice, and transported in insulated containers to the laboratory within three hours, except for packed cell volume, plasma total protein concentration and RBC aggregation which were measured on site within 1 hour from sampling. All measurements were completed within 12 hours following the withdrawal of blood.

To determine the range at which HCT is "optimal" (for protocol see: Nemeth et al., 2009) blood was centrifuged three minutes at 1000 U min^{-1} for plasma separation. Concentrated blood cells and autologous plasma were then carefully re-suspended to obtain 51 PCV values between 5% and 65%, following which WBV was analyzed.

Hematological and biochemical measurements

Hematology was performed by Advia 2120 Haematology Analyser (Siemens, Berlin, Germany) to obtain red blood cell count (RBC, in cells•10^9•L^{-1}), hematocrit (HCT, in %), mean cellular volume (MCV, in fL), mean cellular haemoglobin (MCH, in pg), mean cellular haemoglobin concentration (MCHC, in g d•L^{-1}), and a routine white blood count (WBC, in cells•10^6•L^{-1}). Plasma lactate concentration (LACT, in mmol•L^{-1}) was measured by ACE Alera (Alfa Wassermann B.V., Woerden, The Netherlands). Total protein (TP, in g•L^{-1}) was measured with a refractometer. Packed cell volume (PCV) was measured by centrifugation (JOUAN "Hema C"-centrifuge, Hawksley&Sons, West Sussex, Great Britain).

Hemorheological measurements

Hemorheology included flow curves to provide whole blood viscosity (WBV, in mPa•s) at various shear rates, and RBC aggregation (aggregation indices: M0, M1).

Flow curves were measured using the Physica MCR301 rheometer (A. Paar, Graz, Austria) with cone-plate symmetry under Searle mode. Shear rates between 11.6 and 500 s^{-1} were adjusted for data processing. Isothermal runs were conducted with a logarithmic shear rate ramp. A pre-shear interval of 20 s^{-1} was carried out for 5 s followed by a 1 s rest interval before the measurements started at the lowest shear rate.

RBC aggregation was analyzed by the Myrenne Aggregometer MA1 (Myrenne, Roetgen, Germany). Aggregation indices M0 and M1 were obtained for each sample at room temperature. Aggregation was not verified microscopically. A 30 µL sample was placed in the transparent cone-plate device and spread to a cellular layer. This layer was then sheared at 600 s^{-1} for 10 s to disaggregate all pre-existing aggregates, then abruptly stopped (M0 mode) or rotated at 3 s^{-1} (M1 mode) to allow RBC aggregation. The instrument computes an aggregation index proportional to the area under the light transmission curve, which reflects the amount of plasma gaps due to RBC aggregation. At least five readings were taken for each individual value to obtain mean values for M0 and M1.

Other measurements

As an extra asset, a routine blood chemistry profile was performed to check the health status of the animals prior to the experiment (ACE Alera; Alfa Wassermann B.V., Woerden, The Netherlands). These values are given only in the Supplementary File.

Statistical evaluation

Continuous variables were described by medians and quartiles due to the skewed distribution of most variables. Changes of variables over time were investigated using ANOVA models with animal number as additional factor. Correlations between variables and between time differences of variables are quantified using Spearman correlation coefficients.

Theoretical "optimal HCT" values were calculated from quadratic curves fitted by regression models. Confidence intervals for these values were calculated using the BCa method (Efron and Tibshirani, 1993) where total animals were drawn in each bootstrap step.

No adjustment for testing multiple outcomes was done since the list of outcomes was pre-defined and results are reported for all outcomes irrespective of significance or not. All tests were performed at a two-sided 5% significance level. All computations were done using SAS 9.4, except descriptive graphs for the Supplementary File, which were done using Microsoft Windows Professional Plus 2010 suite for Windows Vista/7.

Results

Hematological values, blood lactate and total protein concentration (Table 1)

During the exercise blood lactate increased from 0.27 (0.2/0.4) to 0.35 mmol•L^{-1} (0.25/0.4), indicating aerobic exercise, and then dropped to 0.21 mmol•L^{-1} (0.15/0.27) following the 30 minutes cooling down period.

Total protein decreased during both the exercise and the cool down period. If an increase of blood volume may be postulated by this effect, this would approximate to 1-2 L in an adult camel. The full routine hematology and blood chemistry results are provided in the Supplementary File (Table A), and were within normal ranges indicating healthy individuals.

Hemorheological values (Table 2)

There was a positive correlation between low and high shear WBV at any occasion ($r>0.6$; $p<0.05$). A strong positive correlation was present between aggregation index M1 and WBV at low (11.6 s^{-1}) and high (500 s^{-1}) shear rates by comparing the time points before and after the exercise (Time 1 – Time 2; $r>0.7$, $p<0.05$), and a strong positive correlation of aggregation index M1 with WBV at high (500 s^{-1}) shear rate by comparing the time points before exercise and after the cool down period (Time 1 – Time 3; $r>0.7$, $p<0.05$). The correlation between PCV and WBV was only present by comparing Time 2 versus Time 3 ($r>0.6$, $p<0.05$). We observed no statistically significant change in PCV, WBV, and RBC aggregation during the experimental protocol.

The complete flow curves at the three time points are provided in the Supplementary File (Figure A). There was a minute decrease of viscosity ratio, which might indicate some structural change in the camels´ blood taken before the exercise and after the cool down period. Measurement of RBC aggregation index M0 gave zero aggregation, whereas the index M1 indicated a minute RBC aggregation predominantly after the exercise.

The theoretical “optimal HCT” values are shown in Figure 1. Original curves are shown in the Supplementary File (Figure B). A comparison between the individual PCV and HCT measurements obtained at the three time points is provided in the Supplementary File, [Figure C (a,b)] in order to show the differences between these methods, presumably due to stacking of RBC at centrifugation.

Theoretical “optimal HCT” decreased continuously with increasing shear rates (Figure 1). At high shear rates, the “optimal HCT” value equaled the resting PCV of the animals investigated. At low shear rates, the PCV of the camels could have been higher by 35 - 58 % to reach the “optimal” range. By comparing these outcomes with the PCV values in the camels during the experiment, we show that at low and intermediate shear rates the actual PCV was lower than its optimal value, whereas at high shear rates the actual PCV matched the theoretical “optimal” value.

Table 1. Packed cell volume (PCV), plasma total protein concentration (TP) and hematologic values before (Time 1), immediately after 30 minutes of trotting (Time 2), and after the 30 minutes cool down period (Time 3). Data are expressed as median and 25%/75% percentile in parentheses.

	Time 1	Time 2	Time 3
PCV (%)	31.0 (31.0/35.0)	32.5 (30.0/6.0)	0.5 (29.5/34.5)
HCT (%)	43 (41/48)	45 (41.5/46)	43 (39/46)
TP ($g \cdot L^{-1}$)	65 (64/67)	64 (62/64)	62 (61/64)
RBC ($cells \cdot 10^{9} \cdot L^{-1}$)	10.3 (9.6/11.2)	10.2 (9.9/10.9)	10.0 (9.5/11.2)
MCV (fL)	42.4 (41.6/43.1)	42.1 (41.3/42.9)	42.0 (41.2/42.8)
MCH (pg)	13.6 (13.4/14.1)	13.7 (13.3/14.1)	13.7 (13.5/14.1)
MCHC ($g \cdot dL^{-1}$)	32.2 (31.9/32.7)	32.5 (32.1/32.9)	32.6 (32.3/32.8)
WBC ($cells \cdot 10^{6} \cdot L^{-1}$)	10.8 (9.0/12.4)	10.6 (8.8/11.8)	10.7 (9.0/12.3)

Table 2. Hemorheologic values before (Time 1), immediately after 30 minutes of trotting (Time 2), and after the 30 minutes cool down period (Time 3). Data are expressed as median and 25%/75% percentile in parentheses.

	Time 1	Time 2	Time 3
WBV 11.6 s^{-1} ($mPa \cdot s$)	6.3 (4.6/9.6)	6.9 (6.6/9.1)	6.3 (5.4/9.9)
WBV 500 s^{-1} ($mPa \cdot s$)	2.7 (2.2/3.5)	3.1 (2.9/3.7)	3.0 (2.6/3.3)
Viscosity ratio	4.1 (2.5/6.4)	4.1 (3.1/5.6)	3.7 (2.8/5.8)
M0	0 (0/0)	0 (0/0)	0 (0/0)
M1	0.7 (0.1/1.8)	1.6 (0.7/3.3)	1.1 (0/3.2)

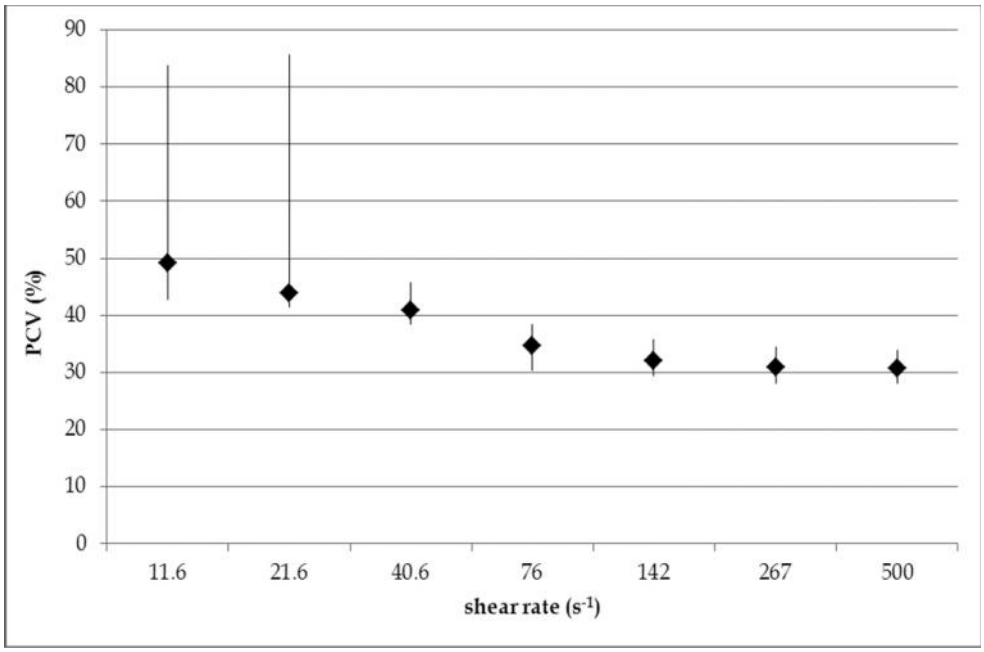

Figure 1. Theoretical "optimal HCT" decrease with increasing shear rates. Values are expressed as median and upper/lower quartile.

Discussion

Camelids are not only perfectly adapted to live in the habitat of arid environments found in deserts and semi-deserts, they are also able to perform remarkably well as dairy camels, transport animals or as racing camels in these challenging conditions. The effects of exposure to ambient heat (Abdalla et al., 2011; Roy and Tiwari, 2010), trypanosoma-infection (Chaudhary and Iqbal, 2000) and physical exercise in general (Bosona et al., 2011; Maloiy et al., 2009), to name a few, are well investigated. With regard to racing camels, it has been described that during a race the increase in HCT is virtually absent, therefore no additional oxygen carrying capacity is being released. This is in stark contrast to racing dogs and Thoroughbred horses (Böning et al., 2011; Sharp, 2012; Stoiber et al., 2005), where significant amounts of RBC are released from the splenic reservoir. If marked increases in HCT during a race are absent in camels, what other physiological responses allow these animals to perform so well?

In trying to find an answer to this question we followed the hypothesis of a theoretical "optimal HCT", where the oxygen transport capacity is at a maximum. At low HCT, any release of RBC into the circulating blood enhances O_2-supply to the muscles, whereas at high pre-existing HCT values, any further increase of HCT leads to an increase in blood viscosity and subsequent reduction of the O_2-supply (Stark and Schuster, 2012). This is in essence expressed through the theoretical "optimal HCT". Nemeth et al. (2009) report a range around a HCT of 45% to be optimal in dogs at shear rates of 90 s^{-1} and 200 s^{-1}, and Bogar et al. (2005) report a range of about 43% at a low shear rate (10 s^{-1}) and 60% at a high shear rate (200 s^{-1}) in healthy human volunteers. WBV is known to influence tissue perfusion through increased venous resistance (Baskurt and Meiselman, 2008; Baskurt et al., 1999; Cabel et al., 1997; Yalcin et al., 2004). During exercise, a negative correlation between the increase in WBV and the decrease of systemic vascular resistance was reported in human beings (Connes et al., 2009; Connes et al., 2012). It has to be kept in mind that the HCT changes dynamically when blood flows through the vascular compartments, leading to a reduction of relative viscosity (the Fahraeus-Lindqvist effect, Gaehtgens, 1981c). Therefore, a consideration of an "optimal HCT" for tissue perfusion is limited to bulk blood flow only. In the smallest vessels there is no bulk blood flow, but single RBC have to pass through and here the consideration of an "optimal HCT" is mute.

In the camels studied the theoretical "optimal HCT" varied with the shear rates measured, as in other species (Bogar et al., 2005; Nemeth et al., 2009). At high shear rates above 100 s^{-1}, where the rheological characteristics of blood change and

generally resemble a more Newtonian behaviour (e.g. fluids without corpuscular components), the theoretical "optimal HCT" settled at a PCV of roughly 30%. Interestingly, the PCV of our camels was perfectly within this range during all three phases of the exercise. At low shear rates, which are present in venules and veins, the theoretical "optimal HCT" was significantly higher than the actual PCV. In working skeletal muscle the movement induced hypaeremia should be increased compared to resting muscle, thus the vasodilatory reserve might be reduced. A high positive difference between the "optimal HCT" compared to the resting HCT is thus a clear benefit. This could also indicate that the HCT in this vascular section could rise even before an increase in viscosity would restrict the blood flow. When camels experience dehydration such a mechanism could eventually prevent blood from becoming sluggish in the venules.

We were surprised by the marked difference between the PCV and HCT values obtained from the individual samples as shown in the Supplementary File, Figure C (a,b). While the PCV was obtained by microcentrifugation, the HCT value was calculated based on the electric resistance detecting method (cell number and volume). The only explanation we can offer is that due to the specific spindle shape of the camel RBC the cellular pellet obtained through microcentrifugation is more dense than in other species. The implication for the present study was that we were required to consistently refer to the PCV values as the cell suspensions for determining the "optimal HCT" were measured by the microcentrifugation method only.

We deemed that the minute changes observed in HCT could not by themselves account for the required increase in muscle oxygenation in responses to exercise, and turned our attention to possible changes in the mechanical properties of the RBC. Based on the available data from Thoroughbred horses, one would expect an increase in WBV, as well as RBC aggregability during submaximal exercise (Stoiber et al., 2005). However, neither was the case in the camels we observed because PCV as well as HCT increased only marginally. There was no statistically significant increase in WBV at the shear rates measured during and after exercise. We also found that RBC aggregability remained essentially unchanged throughout the protocol. With RBC being the blood oxygen store, their distribution to peripheral tissues not only depends on the hemodynamic situation and the geometry of the vascular tree, but is also fine-tuned by the intrinsic RBC properties (Yalcin et al., 2006). The interaction of the flowing blood with the vessel wall (Cokelet and Meiselman, 2007; Kim et al., 2009; Ong et al., 2012), modulates the expression of vasoactive endothelial factors through mechanotransduction of endothelial shear forces (Baskurt et al., 2004; Malek and Izumo, 1992; Moncada et al., 1991; Yalcin et al., 2008). This mechanism is important when the vessel diameter reaches a critical value in comparison to the diameter of the corpuscular parts within the flowing blood. Phase separation then occurs to result in a marginal cell free "gliding layer" for RBC. It is well recognized that the width of this plasma layer is associated with the degree of RBC aggregation (Baskurt and Meiselman, 2008; Namgung et al., 2013; Ong and Kim, 2013; Yalcin et al., 2004; Yalcin et al., 2006). These studies show that the tissue HCT can be modified if RBC have the ability to form aggregates. However, it has to be recognized that such a gliding layer is not constant, but varies with the pulsatility of arterial wall movement and muscle contraction during movement (Zhang et al., 2009).

In our camels, both aggregation indices M0 and M1 remained fairly unchanged in response to exercise. This did not come as a surprise as the RBC of camel are not expected to aggregate due to their spindle-shape, their bi-convex surface probably preventing the formation of substantial aggregates. Although not statistically significant, M1, which reflects aggregation during low shear rate (3 s^{-1}), increased slightly with the exercise. Whether or not this is an artifact due to roof-tile overlay in the rotating shear flow cannot be stated with confidence. Interestingly enough there was a strong correlation between WBV and M1, suggesting that there was some form of organization within the blood sample in relation with the shear flow. It remains to be determined whether in the relative absence of RBC aggregation a phase separation can indeed occur in the camel, or if other mechanisms are in place to aid the microcirculation.

The data presented above suggest that camel do not depend on a rising HCT to perform physically, although it has to be considered that the camels we investigated were only trotting. Median values of the plasma lactate concentration did increase from 0.27 to 0.35 mmol•L^{-1}, suggesting an aerobic exercise in our animals throughout the experimental protocol. A more intensive exercise might have led to a more pronounced change in the parameters observed, particularly the increase in HCT and

RBC aggregation. Increasing whole blood viscosity is a limiting factor for exercise tolerance. A previous study in thoroughbred horses (Stoiber et al, 2004) showed that a rise in WBV during submaximal exercise was evident in well trained horses compared to horses at the beginning of their training. Other studies indicate that such a rise in HCT may disappear in response to physical conditioning (Brun et al, 1998; Neuhaus and Gaethgens, 1994, El-Sayed, 1998; Wood et al., 1991). A rise in blood viscosity was even a significant indicator for overtraining in elite athletes (Benhaddad et al., 1991). In the present study, body weight of the camels, nutritional factors or the hydration status of the animals was not assessed. We need to point out that our investigation was of a discovery nature, as knowledge of the peculiar aspects of camel rheology during exercise performance is limited. Parameters that are associated with the composition of whole blood and the integrity or the regular composition of RBC membranes may thus have influenced our study outcome (Monnier et al., 2000, Sentürk et al., 2001; Varlet-Marie et al., 2003). Usually, plasma volume increases in response to physical exercise (Fellmann, 1992). Blood volumes can be approximated by changes in the TP concentration because of the kinetics of protein synthesis in the liver. In the absence of a protein loss through kidneys or sweating, a decrease of TP indicates a gain in plasma volume. Following this assumption, we estimated an increase in plasma volume of approximately 1-2 L as we indeed found a decrease of plasma total protein concentration after the race. This was accompanied by a certain mobilization of RBC as evidenced by the slight increase of HCT, more than compensating the diluting effect of the compartmental fluid shift. This way, it is important to note that the camels studied not only maintained, but expanded their blood oxygen store in response to the exercise stimulus – an effect that may also be more distinct during a more intensive exercise.

Conclusions

Changes in plasma volume and hemoconcentration during endurance or peak performance exercise, and its impact on blood fluidity, are not as well described in the camel as in other species. The roles of a possible change in hemoconcentration in camels remain uncertain, as the blood viscosity is less dependent on shear rate than in other mammalian species. The data presented suggests that camel do not depend on a high HCT to perform. It remains to be determined whether a phase separation can indeed occur in the camel, or what other mechanisms are in place to aid the microcirculation. In considering the findings it has to be taken into account that our camels were only trotting for a comparatively short distance. It is possible that our results would have been more pronounced if we would have subjected the camels to a more challenging physical exercise. It has to be taken into account that the study was performed at an altitude of 1700 m. Further studies at higher exercise intensity levels, on the temperature- and HCT-dependency of WBV, and on the suspension stability of blood at very low shear rates are required to gain a more comprehensive understanding of this intriguing athlete.

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Author contributions

R. A. designed the study, performed the measurements, wrote the paper, and received funding. A. G. performed the statistical analysis. U. W. was supervisor of the project, established the rheological protocol, and corrected the article.

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