Peplomer bulb shape and coronavirus rotational diffusivity

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ABSTRACT

Recently, the rotational diffusivity of the coronavirus particle in suspension was calculated, from first principles, using general rigid bead-rod theory [M. A. Kanso, Phys. Fluids 32, 113101 (2020)]. We did so by beading the capsid and then also by replacing each of its bulbous spikes with a single bead. However, each coronavirus spike is a glycoprotein trimer, and each spike bulb is triangular. In this work, we replace each bulbous coronavirus spike with a bead triplet, where each bead of the triplet is charged identically. This paper, thus, explores the role of bulb triangularity on the rotational diffusivity, an effect not previously considered. We thus use energy minimization for the spreading of triangular bulbs over the spherical capsid. The latter both translates and twists the coronavirus spikes relative to one another, and we then next arrive at the rotational diffusivity of the coronavirus particle in suspension, from first principles. We learn that the triangularity of the coronavirus spike bulb decreases its rotational diffusivity. For a typical peplomer population of 74, bulb triangularity decreases the rotational diffusivity by 39%.

I. INTRODUCTION

Recently, we calculated the rotational diffusivity of the coronavirus particle in suspension as a function of peplomer population, from first principles, using general rigid bead-rod theory (Fig. 12 of Ref. 1). We did so by beading the capsid and then also by replacing each of its bulbous spikes with a single bead. However, each coronavirus spike is a glycoprotein trimer, and each spike bulb is triangular. In this work, we replace each bulbous coronavirus spike with a bead triplet, where each bead of the triplet is charged identically. This paper, thus, explores the role of bulb triangularity on the rotational diffusivity, an effect not previously considered. We thus use energy minimization for the spreading of triangular bulbs over the spherical capsid. The latter both translates and twists the coronavirus spikes relative to one another, and we then next arrive at the rotational diffusivity of the coronavirus particle in suspension, from first principles. We learn that the triangularity of the coronavirus spike bulb decreases its rotational diffusivity. For a typical peplomer population of 74, bulb triangularity decreases the rotational diffusivity by 39%.

Since each coronavirus spike is a glycoprotein trimer, each spike bulb is triangular (Fig. 14 of Ref. 1). By replacing each coronavirus spike bulb with a single bead (see circle in Fig. 14 of Ref. 1), our prior work neglects this triangularity. In this present work, we replace each bulbous coronavirus spike (Fig. 2) with a bead triplet (Fig. 3), with each bead identical and charged identically. We must, thus, replace the well-known polyhedral solutions to the single-bead Thomson problem with our new solutions to the triple-bead Thomson problem. In this work, we thus use minimum potential energy peplomer arrangements for our coronavirus model particles.

Since coronavirus bulbs are trimers, they not only translate into a set of centroidal positions relative to one another but also twist into a set of orientations relative to one another. Our potential energy minimization for our triply beaded peplomers thus yields both triplet positions and triplet orientations (Fig. 4). This new potential energy minimization yields a set of bead positions for the triply beaded
peplomers whose centroid positions differ, of course, from the bead positions for the singly beaded counterpart of the same \( N_p \). In other words, the polyhedra of centroids differ from the well-known Thomson solutions used in Ref. 1.

The challenge in determining the rotational diffusivity of a virus particle, from first principles, begins with modeling its intricate geometry with beads, locating the position of each bead. Once overcome, the next challenge is to use this geometry to arrive at the transport properties for the SARS-CoV-2 particle. From these, we deepen our understanding of how these remarkable particles align their peplomers both for long enough, and often enough, to infect.1

Whereas our prior work relied on the Thomson solution for point charges (Fig. 1), here, we work with triads of point charges each spaced rigidly and equilaterally (Fig. 4). We, thus, complicate the energy minimization with the length of this equilateral triangle, \( r_A \). From Table X of Ref. 1, mindful of Fig. 8 of Ref. 1, we get

\[
\frac{1}{10} < \frac{r_A}{r_p} \leq \frac{7}{25},
\]

and in this work, we choose \( r_A/r_p = 0.19 \) for our energy minimization. To compare with our previous work, we match the dimensionless virus radius of Fig. 12 of Ref. 1, \( r_v/r_c = 5/4 \). Using the energy...
minimization to arrange and orient the coronavirus spikes relative to one another, we next arrive, from first principles, at the rotational diffusivity of the coronavirus particles with triple beaded peplomers in suspension.

II. METHOD

For this work, we chose general rigid bead–rod theory for its flexibility and accuracy (Sec. I of Refs. 8 and 9). Using general rigid bead–rod theory, we follow the method of Sec. II of Ref. 1 to construct our virus particle from sets of beads whose positions are fixed relative to one another. For example, the SARS-CoV-2 particle geometry is a spherical capsid surrounded by a constellation of protruding peplomers. We take our bead-rod models of virus particles to be suspended in a Newtonian solvent. To any such collection of bead masses, we can associate a moment of inertia ellipsoid (MIE) whose center is the center of mass and whose principal moments of inertia match those of the virus particle. The MIE, thus, determines the orientability of the virus particle, and thus, the virus rotational diffusivity. We use Eqs. (3)–(13) in Ref. 1 for the method of computing the rotational diffusivity (see Footnote 2 of p. 62 of Ref. 10)

\[ D_r \equiv \frac{1}{6} \alpha, \]

or [Eq. (23) of Ref. 1]

\[ \dot{\alpha} D_r = \frac{\nu}{\sqrt{2}}, \]

which we will use for our results below. Symbols, dimensional, or non-dimensional are defined in Table I or Table II, following the companion paper for singly beaded peplomer for SARS-CoV-2 particle.

III. OSCILLATORY SHEAR FLOW

In this paper, we focus on small-amplitude oscillatory shear flow (SAOS). For this flow field, for the molecular definition of small amplitude, general rigid bead–rod theory yields [Eq. (32) of Ref. 1]

\[ \dot{\alpha}^{(g)} \ll \frac{1}{\nu \sqrt{2}}, \]


\[ \eta^{(g)} \equiv \eta - i \eta', \]


\[ \eta' - \eta = \left( \frac{1}{2b/\nu + 1} \right)^{-1} \left( \frac{1}{2b/\nu + 1} + \frac{1}{1 + (\lambda \omega)^2} \right), \]


\[ \eta'' = \eta_0 - \eta = \left( \frac{1}{2b/\nu + 1} \right)^{-1} \frac{\lambda \omega}{1 + (\lambda \omega)^2}, \]

where \( \lambda \omega \) is the Deborah number. In this paper, we plot the real and minus the imaginary parts of the shear stress responses to small-amplitude oscillatory shear flow as functions of frequency, following Ferry (Secs. 2.A.4–2.A.6. of Ref. 13) or Bird et al. (Sec. 4.4 of Ref. 14).

As \( \omega \to 0 \), for the polymer contribution to the zero-shear viscosity, we get

\[ \eta_0 - \eta = \frac{av}{\tau} + b \left[ 1 + \frac{2b}{av} \right] \left( \frac{2b}{av} \right)^{-1}, \]

which we use in the table of Sec. V below.

IV. MODELING OF TRIMERIC PEPLOMER

As shown by Kirchdoerfer, each trimeric peplomer head, consisting of three glycoproteins, is well-approximated by an equilateral...
triangle when viewed along the spike axis. In the general rigid bead-rod model,
this trimer is replaced with a sphere. Here, we approximate the trimer by considering an identical point charge at each vertex of the equilateral triangle.

### A. Kinematics

Let $N_p$ be the number of trimeric peplomers attached to the capsid-sphere $C$ of radius $r_c$. Let $T_i$ denote the equilateral triangle that approximates the trimeric head of the $i$th peplomer. Let the $p_{th}$ vertex of $T_i$ be parameterized by $r_{cr_i}$, where $i = 1...N_p$ and $p = 1, 2, 3$. Let the length of the side of $T_i$, $i = 1...N_p$, be given by $d$. Thus, the vertices of $T_i$ are

$$r_{cr_i} = r_c + \ell, \quad i = 1...N_p.$$

(9)

Let $\ell$ be the length of the spike of each peplomer, with each spike normal to $C$ at the point of contact on $C$. We assume that the centroid of $T_i$ is at the other end of the spike. Therefore, it must lie on the sphere $S$ of radius $r_c = r_c + \ell$,

$$r_{cr_i}^2 (r_{c1} + r_{c2} + r_{c3})^2 = r_c^2, \quad i = 1...N_p.$$

(10)

We also assume that each triangle $T_i$ lies in the tangential plane of the $S$ at its centroid. This implies that normal to the plane of $T_i$ must align with the vector joining the centroid of $T_i$ to the center of $S$,

$$[(r_{c1} - r_{c2}) \times (r_{c1} - r_{c3})] \cdot (r_{c1} + r_{c2} + r_{c3}) = 0,$$

(11)

which simplifies to

$$(r_{c1} \times r_{c2}) \cdot r_{c3} + (r_{c2} \times r_{c3}) \cdot r_{c1} + (r_{c3} \times r_{c1}) \cdot r_{c2} = 0.$$

(12)

### B. Energetics

Let each vertex of each triangle $T_i$, $i = 1...N_p$, be endowed with point charge $Q$. The total electrostatic energy of $N_p$ peplomers, constrained to the sphere $S$ of radius $r_c$, is given by

$$E = \frac{Q}{4\pi \varepsilon r_c} \sum_{i=1}^{N_p} \sum_{j=1}^{N_p} \sum_{k=1}^{3} \sum_{m=1}^{3} \sum_{l=1}^{3} \frac{1}{|r_{c_i} - r_{c_j}|},$$

(13)

where $\varepsilon$ is the dielectric permittivity. Using the constrained minimization approach of Ref. 16, we obtain numerical equilibrium solutions $r_{cr_i}, i = 1...N_p$, and $p = 1, 2, 3$ that locally minimize the energy in Eq. (13) while satisfying the kinematic constraints in Eqs. (9)–(12), for given values of $N_p$. Since the charge $Q$ appears only as a prefactor in Eq. (13), its value plays no role in determining equilibrium solutions.

Our trimeric model amounts to a replacement for the Thompson problem, the objective of which is to find a state that distributes $N_p$ equilateral triads of charges over a unit sphere as evenly as possible, with minimum electrostatic energy. By contrast, Wales’14 distributed $N_p$ single charges, providing solutions for a large set of values of $N_p$.

### V. RESULTS AND CONCLUSION

From Fig. 5, we learn that the detailed triangular structure of the peplomer head and its singly beaded counterpart share the same qualitative behavior. For both, the rotational diffusivity, $\lambda_0 D_r$, descends monotonically with $N_p$. However, the detailed triangular structure of the peplomer head reduces significantly $\lambda_0 D_r$ of the coronavirus particle. Specifically, at the measured peplomer population of $N_p = 74$, we see a reduction in $\lambda_0 D_r$ of 39%. On close inspection, Fig. 5 also reveals

$$\frac{\lambda_0 D_r (3N_p)}{\lambda_0 D_r (N_p)} \approx 1,$$

that is, the dimensionless rotational diffusivity of a coronavirus with $N_p$ singly beaded peplomers has about the same dimensionless rotational diffusivity of a coronavirus with $\frac{1}{2} N_p$ triply beaded peplomers.

From Fig. 6, we learn that the elasticity, $\eta / (\eta_0 - \eta_s)$, of the coronavirus particle suspension is slight and that the detailed triangular structure of the peplomer head slightly reduces this elasticity. From

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**TABLE II. Dimensionless variables and groups.**

| Name                                      | Symbol |
|--------------------------------------------|--------|
| Capsid-sphere                              | $C$    |
| Coefficient in Eq. (3)                     | $\nu$  |
| Coefficient in Eq. (6)                     | $a$    |
| Coefficient in Eq. (10)                    | $b$    |
| Deborah number, oscillatory shear          | $D_e \equiv \lambda_0 a$ |
| Equilateral triangle of $i$th peplomer     | $T_i$  |
| Sphere                                     | $S$    |
| Total number of beads                      | $N$    |
| Total number of capsid beads               | $N_c$  |
| Total number of peplomers                  | $N_p$  |
| Weissenberg number                         | $W_i \equiv \lambda_i^a$ |

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**FIG. 5.** Dimensionless rotational diffusivity $\lambda_0 D_r$ from Eq. (3) vs peplomer population $N_p$ ($N_p = 256$): single (red) and triple beading (blue) corresponds to, respectively, rows 1 and 2 of Table III.
Table III, we see that the corresponding \( b \) is nearly zero so that the polymer contribution to the real part of the complex viscosity is constant, \( (\eta' - \eta) / nkT \lambda = (\eta_0 - \eta) / nkT \lambda = 3/2 \). From Table III, we learn that the detailed triangular structure of the peplomer head increases the relaxation time, \( \lambda \), and thus, decreases the zero-shear viscosity, \( \eta_0 \). From the rightmost column of Table III, we learn that the detailed triangular structure of the peplomer head decreases the zero-shear value of the first normal stress coefficient, \( \Psi_{1,0} \).

Whereas much prior work on fluid physics related to the virus has attacked transmission,\(^{17–41}\) this paper focuses on the \textit{ab initio} calculation of coronavirus transport properties. Specifically, we have determined the rotational diffusivity, the property governing the particle alignment for cell attachment (see Sec. I of Ref.\(^1\)). Although our work is mainly curiosity driven, it may deepen our understanding of drug, vaccine, and cellular infection mechanisms.

Chaurasia et al.\(^{42}\) (see also Chaurasia\(^{43}\)) developed a framework to find equilibrium solutions of a system consisting of flexible structures, specifically charged elastic loops constrained to a sphere. Their framework could be used to model flexible peplomers with uniformly charged heads. We leave this daunting task for a future study.

Since the coronavirus capsid can be ellipsoidal (Fig. 3. of Ref.\(^{44}\)), called pleomorphism, we must eventually consider this too. Whereas this work considered the detailed triangular structure of the peplomer head as triads of three point-charges, we could also consider uniformly charged triangular rigid peplomers constrained to a sphere. By \textit{uniformly charged triangular}, we mean that the charge would be uniformly distributed over the edges of the triangle rather than point charges at its vertices. We leave this task for a later date.

One cognate transport problem is the transient translation and twist of coronavirus spikes rearranging freely under their own
electrostatic repulsions, for instance, the transient following the extraction of a single spike. This paper is, of course, silent on this interesting problem, which we leave for another day.

As in our previous work,1 we have used repulsions of charged particles over the surfaces of spheres for both the capsid and the peplomer heads of the coronavirus to arrive at its transport properties. It has not escaped our attention that our solutions to the Thomson problem can also be used to calculate the Young’s modulus of the corona-virus particle [Eq. (3a) of Ref. 45] and that by extension this Young’s modulus will depend upon peplomer population. We leave this calculation for another day. When using the references cited herein, it is best to be mindful of corresponding ganged errata in Ref. 46.

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DATA AVAILABILITY

The data that support the findings of this study are available within the article.

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9

\[ \frac{1}{2} L \cdot \left( \frac{L}{C_0} \right)^\frac{1}{2} \] in Table 16.4–1, under entry “length of rod” should be “bead number”.
10

In Table IV, Macromolecule 21 entry should be “Multibead rods of length L + d.”
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