
This copy is for your personal, non-commercial use only.

If you wish to distribute this article to others, you can order high-quality copies for your colleagues, clients, or customers by [clicking here](#).

Permission to republish or repurpose articles or portions of articles can be obtained by following the guidelines [here](#).

The following resources related to this article are available online at www.sciencemag.org (this information is current as of April 24, 2014):

Updated information and services, including high-resolution figures, can be found in the online version of this article at:

<http://www.sciencemag.org/content/332/6027/339.full.html>

Supporting Online Material can be found at:

<http://www.sciencemag.org/content/suppl/2011/04/14/332.6027.339.DC2.html>

<http://www.sciencemag.org/content/suppl/2011/04/12/332.6027.339.DC1.html>

A list of selected additional articles on the Science Web sites **related to this article** can be found at:

<http://www.sciencemag.org/content/332/6027/339.full.html#related>

This article **cites 9 articles**, 2 of which can be accessed free:

<http://www.sciencemag.org/content/332/6027/339.full.html#ref-list-1>

This article has been **cited by** 1 articles hosted by HighWire Press; see:

<http://www.sciencemag.org/content/332/6027/339.full.html#related-urls>

This article appears in the following **subject collections**:

Engineering

<http://www.sciencemag.org/cgi/collection/engineering>

Physics

<http://www.sciencemag.org/cgi/collection/physics>

A Bicycle Can Be Self-Stable Without Gyroscopic or Caster Effects

J. D. G. Kooijman,¹ J. P. Meijaard,² Jim M. Papadopoulos,³ Andy Ruina,^{4*} A. L. Schwab¹

A riderless bicycle can automatically steer itself so as to recover from falls. The common view is that this self-steering is caused by gyroscopic precession of the front wheel, or by the wheel contact trailing like a caster behind the steer axis. We show that neither effect is necessary for self-stability. Using linearized stability calculations as a guide, we built a bicycle with extra counter-rotating wheels (canceling the wheel spin angular momentum) and with its front-wheel ground-contact forward of the steer axis (making the trailing distance negative). When laterally disturbed from rolling straight, this bicycle automatically recovers to upright travel. Our results show that various design variables, like the front mass location and the steer axis tilt, contribute to stability in complex interacting ways.

A bicycle and rider in forward motion balance by steering toward a fall, which brings the wheels back under the rider [supporting online material (SOM) text S1 and S2] (1). Normally, riders turn the handlebars with their hands to steer for balance. With hands off the handlebars, body-leaning relative to the bicycle frame can also cause appropriate steering. Amazingly, many moving bicycles with no rider can steer themselves so as to balance—likewise with a rigid rider whose hands are off the handlebars. For example, in 1876, Spencer (2, 3) noted that one could ride a bicycle while lying on the seat with hands off, and the film *Jour de Fête* by Jacques Tati, 1949, features a riderless bicycle self-balancing for long distances. Suspecting that bicycle rideability, with rider control, is correlated with self-stability of the passive bicycle, much theoretical research has focused on this bicycle self-stability.

The first analytic predictions of bicycle self-stability were presented independently by French mathematician Emmanuel Carvallo (1897) (4) and Cambridge undergraduate Francis Whipple (1899) (3, 5). In their models and in this paper, a bicycle is defined as a three-dimensional mechanism (Fig. 1A) made up of four rigid objects (the rear frame with rider body B, the handlebar assembly H, and two rolling wheels R and F) connected by three hinges. The more complete Whipple version has 25 geometry and mass parameters. Assuming small lean and steer angles, linear and angular momentum balance—as constrained by the hinges and rolling contact—lead to a pair of coupled second-order linear differential equations for leaning and steering (SOM text S3) (6). Solutions of these equations show that after small perturbations, the motions of a bicycle may exponentially decay in time to upright right straight-ahead motion (asymptotic stability).

This stability typically can occur at forward speeds v near to \sqrt{gL} , where g is gravity and L is a characteristic length (about 1 m for a modern bicycle). Limitations in the model include assumed linearity and the neglect of motions associated with tire and frame deformation, tire slip, and play and friction in the hinges. Nonetheless, modern experiments have demonstrated the accuracy of the Whipple model for a real bicycle without a rider (7).

The simple bicycle model above is energy-conserving. Thus, the asymptotic stability of a bicycle, that the lean and steer angles exponentially decay to zero after a perturbation, is jarring to those familiar with Hamiltonian dynamics. But because of the rolling (non-holonomic) contact of the bicycle wheels, the bicycle—although energy-conserving—is not Hamiltonian, and it is possible for a subset of variables to have exponential stability in time (6, 8). There is no contradiction between exponential decay and energy conservation because for a bicycle, the energy lost from decaying steering and leaning motions goes to increase the forward speed. Unresolved, how-

ever, is the cause of bicycle self-stability. In some sense, perhaps, a self-stable bicycle is something like a system with control, albeit self-imposed.

Rider-controlled stability of bicycles is indeed related to their self-stability. Experiments like those of Jones (9) and R. E. Klein (10) show that special experimental bicycles that are difficult for a person to ride, either with hands on or off, tend not to be self-stable. Both no-hands control (using body bending) and bicycle self-stability depend on “cross terms,” in which leaning causes steering or vice versa. The central question about what causes self-stability is thus reduced to, what causes the appropriate coupling between leaning and steering? The most often discussed of the coupling effects are those due to front-wheel gyroscopic torque and to caster effects from the wheel trailing behind the steer axis. Trail (or “caster trail”) is the distance c that the ground contact point trails behind the intersection of the steering axis with the ground (Fig. 1A).

There is near universal acceptance that either spin angular momentum (gyroscopic effect) or trail, or both, are necessary for bicycle self-stability (3). Active steering of a bicycle front wheel causes a gyroscopic torque on an upright frame and rider. Because the front wheel is relatively light as compared with the more massive bicycle and rider, the effect of this gyroscopic torque on the lean is generally small (SOM text S1) (11). However, coupling the other way—the effect of active bicycle-leaning on hands-free steering—is nonnegligible. For example, when the bicycle has a lean rate to the right the front axle also has a lean rate to the right, and the spinning wheel exerts a clockwise (looking down) reactive torque carried at least in part by the handlebar assembly. This reaction torque tends to turn the handlebars rightward. Thus, the common explanation of no-hands rider control: To steer to the right, the rider bends her upper body to the left, tilting the bicycle and wheels rightward (5). The bicycle

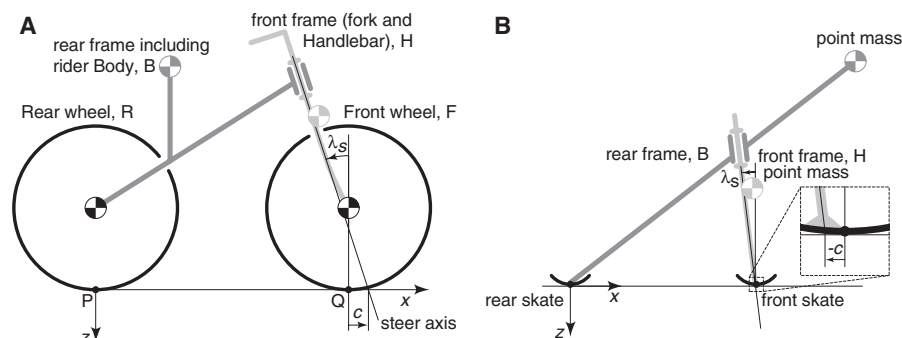


Fig. 1. (A) The bicycle model consists of two interconnected frames, B and H, connected to two wheels, R and F. The model has a total of 25 geometry and mass-distribution parameters. Central here are the rotary inertia I_{yy} of the front wheel, the steer axis angle (“rake”) λ_s , and the trail distance c (positive if contact is behind the steer axis). Depending on the parameter values, as well as gravity g and forward speed v , this bicycle can be self-stable or not. (B) A theoretical TMS bicycle is a special case. It is described with only nine free parameters (eight plus trail). The wheels have no net rotary inertia and thus function effectively as ice skates. The two frames each have a single point mass and no mass moments of inertia. A heavy point mass on the rear skate at the ground contact point can prevent the bicycle from tipping over forward; because it has no effect on the linearized dynamics, it is not shown. Even with negative trail ($c < 0$; inset), this non-gyroscopic bicycle can be self-stable.

¹Department of Mechanical Engineering, Delft University of Technology, Delft 2628 CD, Netherlands. ²Department of Engineering Technology, University of Twente, Enschede 7500 AE, Netherlands. ³Department of Engineering and Technology, University of Wisconsin–Stout, Menomonie, WI 54751, USA. ⁴Department of Mechanical Engineering, Cornell University, Ithaca, NY 14853, USA.

*To whom correspondence should be addressed. E-mail: ruina@cornell.edu.

handlebars, considered as freely rotating on the steer axis and forced by the gyroscopic front wheel, thus initially turn rightward. Such leaning-induced steering can be used for rider control of balance. Likewise, this gyroscopic coupling also contributes to a forward-moving passive bicycle self-steering toward a fall (12).

The most thorough discussion of the necessity of gyroscopic coupling of leaning to steering for bicycle self-stability is in the bicycle chapter of the fourth volume of the gyroscope treatise by Klein and Sommerfeld (11, 13). They took the example bicycle parameters from Whipple and eliminated just the spin angular momentum of the wheels. Using their own linearized dynamic stability analysis of the Whipple model, Klein and Sommerfeld concluded that, "... in the absence of gyroscopic actions, the speed range of complete stability would vanish" [(11) p. 866] and make what appears to be a strong general claim about bicycles: "The gyroscopic action, in spite of its smallness, is necessary for self-stability" [(11) p. 866].

They emphasized that the gyroscopic torque does not apply corrective lean torques to a bicycle directly, as others seem to have thought (14). Rather, through the gyroscopic torque, leaning causes steering, which in turn causes the righting accelerations: "The proper stabilizing force, which overwhelms the force of gravity, is the centrifugal force, and the gyroscopic action plays the role of a trigger" [(11) p. 881].

In Jones's famous search for an unrideable bicycle (URB) (9), he added a counter-rotating disk to the handlebar assembly, canceling the gyroscopic self-steering torque of the front wheel. He could still (barely) ride such a nongyro bicycle using no hands. Jones rightly deduced that the gyroscopic effect discussed in (11) was not the only coupling between leaning and steering. Jones emphasized the importance of the front-wheel ground contact being behind the steering axis (positive trail, $c > 0$) (Fig. 1A). Even though the front forks of

modern bicycles are typically bent forward slightly, with the wheel-center forward of the steering axis, all modern bicycles still have positive trail (typically from 2 to 10 cm on modern bicycles) because of the steering axis tilt $\lambda_s > 0$. When Jones modified his bicycle by placing the front-wheel ground contact in front of the steer axis (negative trail, $c < 0$), he could not ride using no hands.

In Jones's view, a bicycle wheel is in part like a caster wheel on a shopping cart, with the wheel trailing behind a vertical pivot axis. If a modern bicycle was rolled forward by guiding the rear frame in a straight line while it was held rigidly upright, the front wheel would quickly self-center like a shopping-cart caster. Jones noted, "The bicycle has only geometrical castor [sic] [trail] stability to provide its self-centering" [(9) p. 40]. Jones's main focus was a second trail effect: The vertical ground contact force on the front-wheel-ground contact point exerts a steering torque on a leaned bicycle even when the bicycle is steered straight. Jones calculated the steer torque caused by lean as a derivative of a static potential energy, neglecting the weight of the front assembly. If a typical modern bicycle is firmly held by the rear frame, leaned to the right, and pressed down hard, then the vertical ground contact force on the front wheel causes a rightward steering torque on the handlebars. The Jones torque can be felt on a normal bicycle by riding in a straight line and bending your upper body to the left, leaning the bicycle to the right: To maintain a straight path, the hands must fight the Jones torque and apply a leftward torque to the handlebars. According to Jones, this torque causes steering toward a fall only when the trail is positive. When the trail is zero, Jones's theory predicts no self-correcting steer torque. Jones seems to conclude that no-hands control authority (the ability to cause steering by body bending) and self-stability both depend on positive trail. A mixture of the two mechanisms Jones discusses certainly suggests that trail is a key part of bicycle stability.

Following Klein and Sommerfeld and Jones, it has become common belief that steering is stable because the front-wheel-ground contact drags behind the steering axis, and leaning is stable because some mixture of gyroscopic torques and trail causes an uncontrolled bicycle to steer in the direction of a fall (3).

Are gyroscopic terms or positive trail, together or separately, really either necessary or sufficient for bicycle self-stability? Following Carvallo, Whipple, Klein and Sommerfeld, and others since [see history in (6)], we began with the linearized equations of motion. Using the numerical values from the benchmark example in (6) and setting the gyroscopic terms to zero, we found that self-stability is lost (SOM text S6.1, which is similar to the result of Klein and Sommerfeld for the Whipple parameters). However, we also found bicycle designs that are self-stable even without gyroscopic terms.

The conflict with Klein and Sommerfeld is partly resolved by noting sign errors in their key stability term (3). Despite their calculation errors, the Whipple bicycle with Whipple's example parameters does indeed lose self-stability when the gyro terms are set to zero. But with their incorrect expressions, Klein and Sommerfeld could make slightly more general claims that are not valid when the sign errors are corrected (3). Whatever generality Klein and Sommerfeld intended (their wording is ambiguous), their result does not apply to bicycles in general.

Similarly, Jones's simplified static-energy calculation seems incomplete in the context of a dynamical system, such as the Whipple and Carvallo models. Jones's static energy calculation only calculates (incompletely) one term, $K_{0\delta_0}$, of the full dynamics equations (3, 6). In a full dynamic analysis, $K_{0\delta_0}$ does not predict the steering of a falling bicycle (3). For example, that term can be nonzero for a bicycle that falls with no self-corrective steering at all. And just as for the gy-

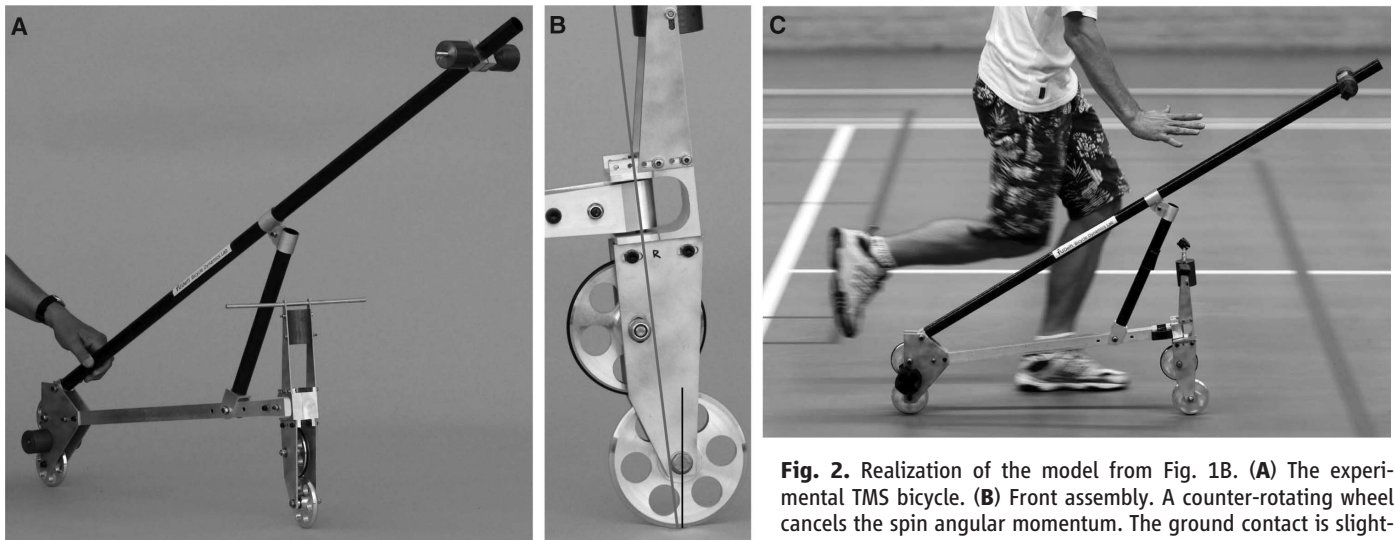


Fig. 2. Realization of the model from Fig. 1B. (A) The experimental TMS bicycle. (B) Front assembly. A counter-rotating wheel cancels the spin angular momentum. The ground contact is slightly ahead of the intersection of the long steer axis line with the

ground, showing the small negative trail (movie S3). (C) Self-stable experimental TMS bicycle rolling and balancing [photo for (C) by S. Rentmeester/FMAX].

roscopic term, we can find designs with zero or negative trail that we predict are self-stable (SOM text S6.2).

In contrast to the conventional claims above for the necessity of gyroscopic terms and trail, we have found no rigorous reasoning that demands either. To understand better what is needed for self-stability, we eliminated as many bicycle parameters as possible (15). Most centrally, we eliminated the gyroscopic terms and set the trail to zero ($c = 0$). We also reduced the mass distribution to just two point masses: one for the rear frame B and one for the steering assembly H (Fig. 1B). With these theoretical parameters, the wheels—having no net spin angular momentum—are mechanically equivalent to skates. These simplifications reduce the number of parameters from Whipple's 25 to a more manageable eight.

Stability analysis of this theoretical two-mass-skate (TMS) bicycle model (SOM text S7), confirmed by means of numerical solution of the governing differential equations, shows that neither gyroscopic terms nor positive trail are needed for self-stability [Routh-Hurwitz analysis shows that all eigenvalues of the theoretical TMS bicycle can have negative real parts at some forward speeds (16)].

We used the stable theoretical TMS bicycle parameters as a basis for building an experimental TMS bicycle (Fig. 2A and SOM text S8 and S9). We used small wheels to minimize the spin angular momentum. To further reduce the gyroscopic terms, following Jones we added counter-spinning disks that rotate backward relative to the lower wheels (Fig. 2B and movie S2). The experimental TMS bicycle was built to have a slightly negative trail ($c = -4 \text{ mm} < 0$) (movie S3). Although the experimental TMS bicycle

looks like a folding scooter, it is still a bicycle (two wheels, two frames, and three hinges).

Because all physical objects have distributed mass, the measured parameters of the experimental TMS bicycle were necessarily slightly different from those of the theoretical design, which was based on point masses. Using measured parameters, we calculated the stability plot of Fig. 3A (SOM text S7 and S8). For rolling speeds greater than 2.3 m/s, all eigenvalues have negative real parts (implying self-stability).

After an initial forward push, the coasting experimental TMS bicycle (Fig. 2C) would remain upright before it slowed down to about 2 m/s (SOM text S10 and S11 and movie S1). As it slowed below 2 m/s, the bicycle would begin to fall. In a perturbation experiment, the stable coasting bicycle ($v > 2.3 \text{ m/s}$) was hit sideways on the frame, causing a jump in the lean rate, followed by a recovery to straight-ahead upright rolling.

The lean and yaw rates were measured (telemetered). A data set was compared with theory in Fig. 3B (movie S4). One difference between experiment and theory is lateral wheel slip at the initial perturbation, which caused an initial jump in the measured yaw rate (Fig. 3B, triangles in the first 0.25 s). The theoretical model assumed no slip. High-speed video (movie S4) also shows a 20-Hz shimmy, which is due at least in part to unmodeled steering axis play (SOM text S11). Nonetheless, after the slipping period—even with the shimmy—the data reasonably track the low-dimensional linear model's predictions.

Both the theoretical analysis and physical experiment show that neither gyroscopic torques nor trail are necessary for bicycle self-stability. Nor are they sufficient. Many bicycle designs with gyroscopic front wheels and positive trail are unstable

at every forward speed (SOM text S6.3). Also, all known bicycle and motorcycle designs lose self-stability at high speeds because of gyroscopic terms [for example, (6)]. In contrast, the TMS bicycle does not have gyroscopic terms and is predicted to maintain stability at high speeds.

With no gyroscopic torque and no trail, why does our experimental TMS bicycle turn in the direction of a fall? A general bicycle is complicated, with various terms that can cause the needed coupling of leaning to steering. Only some of these terms depend on positive trail or on positive spin angular momentum in the front wheel. In the theoretical and experimental TMS designs, the front assembly mass is forward of the steering axis and lower than the rear-frame mass. When the TMS bicycle falls, the lower steering-mass would, on its own, fall faster than the higher frame-mass for the same reason that a short pencil balanced on end (an inverted pendulum) falls faster than a tall broomstick (a slower inverted pendulum). Because the frames are hinged together, the tendency for the front steering-assembly mass to fall faster causes steering in the fall direction. The importance of front assembly mass for Jones-like static torques has been noted before (8, 17, 18).

Why does this bicycle steer the proper amounts at the proper times to assure self-stability? We have found no simple physical explanation equivalent to the mathematical statement that all eigenvalues must have negative real parts (SOM text S4). For example, turning toward a fall is not sufficient to guarantee self-stability. For various candidate simple sufficient conditions X for stability, we have found designs that have X but that are not self-stable. For example, we have found bicycles with gyroscopic wheels and positive trail that are not stable at any speed (SOM text S6.3). We also have found no simple necessary conditions for self-stability. Besides the TMS design with no gyroscope and negative trail, we have found other counterexamples to common lore. We have found a bicycle that is self-stable with rear-wheel steering (SOM text S6.7). We also found an alternative theoretical TMS design that has, in addition to no-gyro and negative trail, also a negative head angle ($\lambda_s < 0$) (SOM text S6.6).

Are there any simply described design features that are universally needed for bicycle self-stability? Within the domain of our linearized equations, we have found one simple necessary condition (SOM text S5): To hold a self-stable bicycle in a right steady turn requires a left torque on the handlebars. Equivalently, if the hands are suddenly released from holding a self-stable bicycle in a steady turn to the right, the immediate first motion of the handlebars will be a turn further to the right. This is a rigorous version of the more general, as-yet-unproved claim that a stable bicycle must turn toward a fall.

Another simple necessary condition for self-stability is that at least one factor coupling lean to steer must be present [at least one of $M_{\delta\phi}$, $C_{\delta\phi}$, or $K_{\delta\phi}$ must be nonzero (SOM text S3)]. These coupling terms arise from combinations of trail,

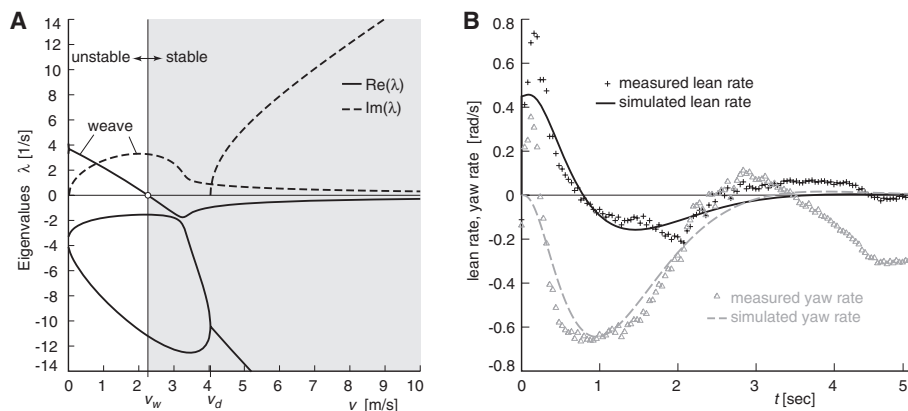


Fig. 3. (A) Stability plot for the experimental TMS stable bicycle. Solutions of the differential equations are exponential functions of time. Stability corresponds to all such solutions having exponential decay (rather than exponential growth). Such decay only occurs if all four of the eigenvalues λ_i (which are generally complex numbers) have negative real parts. The plot shows calculated eigenvalues as a function of forward speed v . For $v > 2.3 \text{ m/s}$ (the shaded region), the real parts (solid lines) of all eigenvalues are negative (below the horizontal axis), and the bicycle is self-stable. (B) Transient motion after a disturbance for the experimental TMS bicycle. Measured and predicted lean and yaw (heading) rates of the rear frame are shown. The predicted motions show the theoretical (oscillatory) exponential decay. Not visible in these plots, but visible in high-speed video (movie S4), is a 20-Hz shimmy that is not predicted by the low-dimensional linearized model (SOM text S10 and S11).

spin momentum, steer axis tilt, and center of mass locations and products of inertia of the front and rear assemblies.

Although we showed that neither front-wheel spin angular momentum nor trail are necessary for self-stability, we do not deny that both are often important contributors. But other parameters are also important, especially the front-assembly mass distribution, and all of the parameters interact in complex ways. As a rule, we have found that almost any self-stable bicycle can be made unstable by misadjusting only the trail, or only the front-wheel gyro, or only the front-assembly center-of-mass position. Conversely, many unstable bicycles can be made stable by appropriately adjusting any one of these three design variables, sometimes in an unusual way. These results hint that the evolutionary, and generally incremental, process that has led to common present bicycle designs might not yet have explored potentially useful regions in design space.

References and Notes

- W. J. M. Rankine, *The Engineer* **28**, 79 (in five parts) (1869).
- C. Spencer, *The Modern Bicycle* (Frederick Warne and Co., London, 1876), pp. 23–24.
- J. P. Meijaard, J. M. Papadopoulos, A. Ruina, A. L. Schwab, <http://ecommons.library.cornell.edu/handle/1813/22497> (2011).
- E. Carvallo, *Théorie du Mouvement du Monocycle et de la Bicyclette* (Gauthier-Villars, Paris, France, 1899).
- F. J. W. Whipple, *Quarterly Journal of Pure and Applied Mathematics* **30**, 312 (1899).
- J. P. Meijaard, J. M. Papadopoulos, A. Ruina, A. L. Schwab, *Proc. R. Soc. Lond. A* **463**, 1955 (2007).
- J. D. G. Kooijman, A. L. Schwab, J. P. Meijaard, *Multibody Syst. Dyn.* **19**, 115 (2008).
- J. I. Neimark, N. A. Fufaev, *Dynamics of Nonholonomic Systems* (Nauka, Moscow, 1967) [J. R. Barbour, transl. (American Mathematical Society, Providence, RI, 1972)].
- D. E. H. Jones, *Phys. Today* **23**, 34 (1970) [reprinted by *Phys. Today* **59**, 9 (2006), pp. 51–56].
- K. J. Åström, R. E. Klein, A. Lennartsson, *IEEE Contr. Syst. Mag.* **25**, 26 (2005).
- F. Klein, A. Sommerfeld, *Über die Theorie des Kreisels* (Teubner, Leipzig, 1910).
- J. A. Griffiths, *Proc. Inst. Mech. Eng.* **37**, 128 (1886).
- In the preface to (11), the authors credit Fritz Noether for the ideas in the bicycle chapter.
- W. Thomson, *Popular Lectures and Addresses* (Macmillan, London, 1889), **1**, pp. 142–146.
- J. M. Papadopoulos, Bicycle steering dynamics and self-stability: A summary report on work in progress (1987), Internal report from the Cornell Bicycle Research Project; available at http://ruina.tam.cornell.edu/research/topics/bicycle_mechanics/bicycle_steering.pdf.
- E. J. Routh, *Proc. Lond. Math. Soc.* **1**, 97 (1873).
- R. N. Collins, thesis, University of Wisconsin, Madison, WI (1963).
- C. Chateau, *La Nature* **20**, 353 (1892).
- R. S. Hand helped with the theory and experiments; A. Dressel helped with the eigenvalue analysis; J. van Frankenhuyzen helped with designing the experimental machine; and J. Moore helped with conducting the experiments. The manuscript was improved by comments from M. Broide, M. Cook, A. Dressel, J. Guckenheimer, R. Klein, D. Limebeer, C. Miller, J. Moore, R. Pohl, L. Schaffer, and D. van Nieuhuys. The research was initially supported by a NSF Presidential Young Investigators award to A.R. The original theory was mostly by J.M.P. with later refinement by A.L.S. J.P.M. found the error in (11). Experiments were performed mostly by J.D.G.K. and A.L.S. Writing was done mostly by A.R. and A.L.S.

Supporting Online Material

www.sciencemag.org/cgi/content/full/332/6027/339/DC1
Materials and Methods
SOM Text S1 to S11
Figs. S1 to S19
Tables S1 to S4
References
Movies S1 to S4

20 December 2010; accepted 10 March 2011
10.1126/science.1201959

DNA Origami with Complex Curvatures in Three-Dimensional Space

Dongran Han,^{1,2*} Suchetan Pal,^{1,2} Jeanette Nangreave,^{1,2} Zhengtao Deng,^{1,2} Yan Liu,^{1,2*} Hao Yan^{1,2*}

We present a strategy to design and construct self-assembling DNA nanostructures that define intricate curved surfaces in three-dimensional (3D) space using the DNA origami folding technique. Double-helical DNA is bent to follow the rounded contours of the target object, and potential strand crossovers are subsequently identified. Concentric rings of DNA are used to generate in-plane curvature, constrained to 2D by rationally designed geometries and crossover networks. Out-of-plane curvature is introduced by adjusting the particular position and pattern of crossovers between adjacent DNA double helices, whose conformation often deviates from the natural, B-form twist density. A series of DNA nanostructures with high curvature—such as 2D arrangements of concentric rings and 3D spherical shells, ellipsoidal shells, and a nanoflask—were assembled.

DNA nanotechnology can now be used to assemble nanoscale structures with a variety of geometric shapes (1–12) [for a recent review, see (13)]. Conventionally, a series of B-form double helices are brought together and arranged with their helical axes parallel to one another. The structure is held together by crossovers between neighboring helices, and the allowed crossover points are based on the pre-existing structural characteristics of B-form DNA. Many DNA nanostructures are variations of polygonal shapes and, although this level of complexity has been sufficient for many purposes, it remains a challenge to mimic the elaborate geom-

etries in nature because most biological molecules have globular shapes that contain intricate three-dimensional (3D) curves. Here, we reveal a DNA origami design strategy to engineer complex, arbitrarily shaped 3D DNA nanostructures that have substantial intrinsic curvatures. Our approach does not require strict adherence to conventional design “rules” but instead involves careful consideration of the ideal placement of crossovers and nick points into a conceptually prearranged scaffold to provide a combination of structural flexibility and stability.

The scaffolded DNA origami folding technique, in which numerous short single strands of DNA (staples) are used to direct the folding of a long single strand of DNA (scaffold), is thus far one of the most successful construction methods based on parallel, B-form DNA (14). The most commonly used scaffold (M13) is ~7000 nucleotides (nts) long and is routinely used to construct

objects with tens to hundreds of nanometer dimensions. Several basic, geometric 3D shapes such as hollow polygons and densely packed cuboids have been demonstrated, as well as a few examples of more complex structures, including a railed bridge and slotted or stacked crosses (15–17). The biggest limitation with conventional, block-based DNA origami designs is the level of detail that can be achieved. Analogous to digitally encoded images, DNA origami structures are usually organized in a finite, raster grid, with each square/rectangular unit cell within the grid (pixel) corresponding to a certain length of double-helical DNA. The target shape is achieved by populating the grid with a discrete number of DNA pixels (for most origami structures, each DNA pixel has a parallel orientation with respect to the other pixels) in a pattern that generates the details and curves of the shape. However, as with all finite pixel-based techniques, rounded elements are approximated and intricate details are often lost.

Recently, Shih and co-workers reported an elegant strategy to design and construct relatively complex 3D DNA origami nanostructures that contain various degrees of twist and curvatures (18). This strategy uses targeted insertion and deletion of base pairs (bps) in selected segments within a 3D building block (a tightly cross-linked bundle of helices) to induce the desired curvature. Nevertheless, it remains a daunting task to engineer subtle curvatures on a 3D surface. Our goal is to develop design principles that will allow researchers to model arbitrary 3D shapes with control over the degree of surface curvature. In an escape from a rigid lattice model, our versatile strategy begins by defining the desired surface features of a target object with the scaffold.

¹The Biodesign Institute, Arizona State University, Tempe, AZ 85287, USA. ²Department of Chemistry and Biochemistry, Arizona State University, Tempe, AZ 85287, USA.

*To whom correspondence should be addressed. E-mail: hao.yan@asu.edu (H.Y.); dongran.han@asu.edu (D.H.); yan_liu@asu.edu (Y.L.)