



Nanoscale

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Journal:	<i>Nanoscale</i>
Manuscript ID	NR-ART-11-2023-006010.R1
Article Type:	Paper
Date Submitted by the Author:	31-Mar-2024
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Tri-State Logic Computation by Activating DNA Origami Chain

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Abstract

The invention of DNA nanotechnology has enabled molecular computation as a promising substitute for traditional semiconductors which are limited to two-dimensional architectures and by heating problems resulting from densification. Current studies of logic gates achieved by DNA molecules are predominately focused on two-state operations (AND, OR, etc.); however, realizing tri-state logic (high impedance Z) in DNA computation is understudied. Here we actively fold DNA origami chain-like hinged rods to induce conformational changes that return tri-state logic signals. We use rigid six helix-bundle (6HB) DNA origami to self-assemble a linear trimer chain as a circuit platform with functional single-stranded (ss) DNA near each semi-flexible hinge. The presence or absence of ssDNA enable and input strands allows hybridization to take place at the hinges, activating one-fold (0) or two-folds (1) from the straight linear geometry (defined as High-Z) of the trimer chain. We design two different tri-state logic gate platforms, buffer and inverter, with corresponding enable/input ssDNA to unambiguously return tri-state signals, characterized by Atomic Force Microscopy (AFM) and/or Agarose gel electrophoresis (GEL). Our work on tri-state logic significantly enhances DNA computation beyond the current two-state Boolean logic with both research and industrial applications, including cellular treatments and living matter utilizing the biocompatibility of DNA molecules.

Main Text

With the end of rapid growth in silicon hardware and Moore's Law there is a renewed interest in DNA computation with a prospective toward logic operations at the molecular level facilitated by DNA nanotechnology [1-22]. Another advantage of organic DNA computation [23-36] compared to inorganic silicon semiconductor is compatibility with living matter. So far the DNA computation community has been primarily focused on studying two-state devices essential to Boolean logic operations. In our work, we aim to introduce tri-state logic DNA computation with the outlook of implementing shared communication lines by multiple devices without causing interference. We've realized non-interference in logic computation taking advantages of the high programmability and specific binding of non-crosstalk DNA sequences.

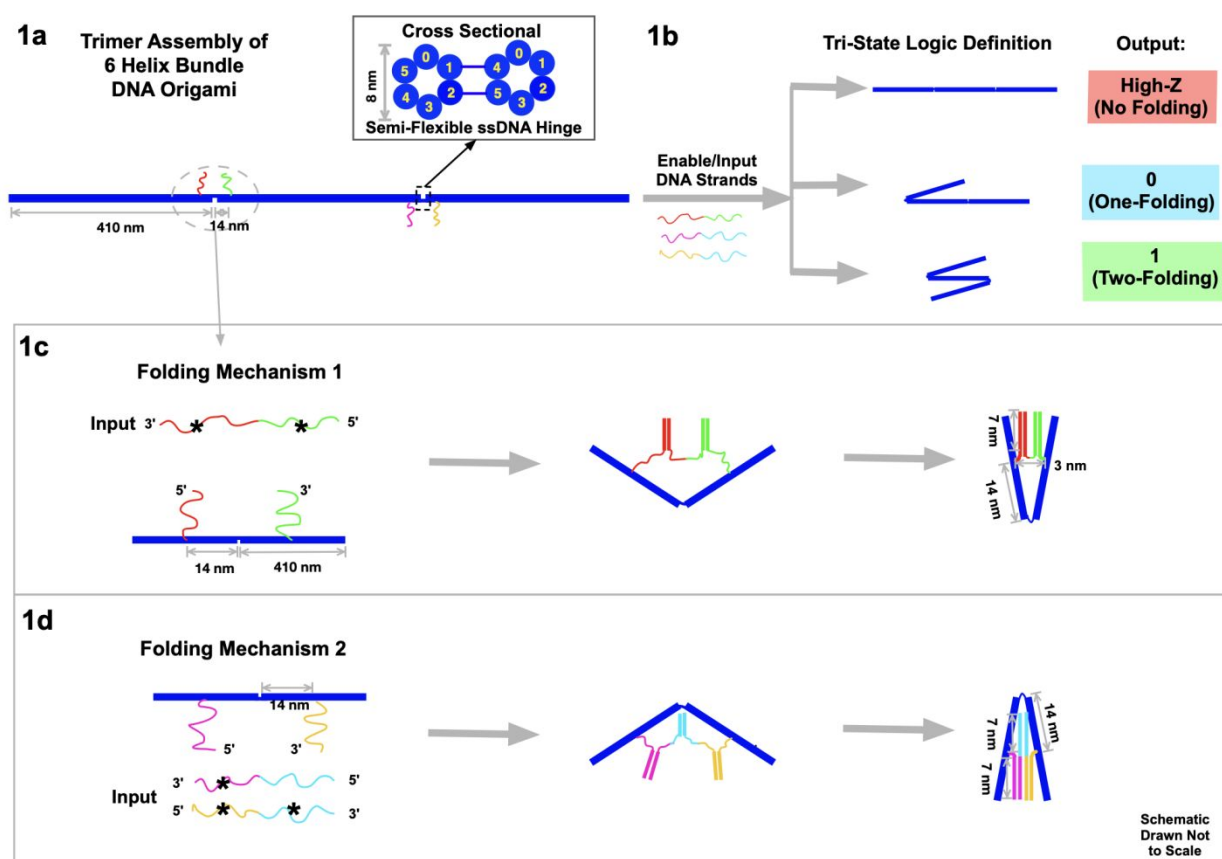


Figure 1. Schematics of experimental designs. **a)** The platform design for our DNA circuits is based on three six-helix bundles (6HB) DNA origami with connected by two hinges and functional sticky ends. **b)** The output signals of our tri-state logic gates are high impedance (no-folds), zero (one-fold), and 1 (two-folds). **c)** The folding mechanism of the first type. An input strand hybridizes to and links the sticky ends to activate the folding of a 6HB

dimer hinge. Colored strands with a “*” are complementary to strands of the same color. **d)** The folding mechanism of the second type. Two input (or enable) strands are required to activate folding of the 6HB dimer structure.

DNA nanotechnology has enabled the construction of complex nano- and micro-scale structures with nanometer-precision, including machines and motors fueled by DNA hybridization [1-3, 13]. Here we design a rod-like 6HB DNA origami, 410 nm long and 8 nm thick, and then self-assemble three of them into a chain-like construct (Fig. 1a) to act as the circuit platform. The axial connection between the three 6HBs contains two semiflexible hinges, 3-base-ssDNA strands. The hinges are rigid enough to align the rods linearly yet flexible enough to be folded by DNA hybridization forces on the two ssDNA. These two non-complementary strands are situated on either side of each hinge, 14 nm from the hinge center. When additional ssDNA strands are added to the DNA origami trimer platform, hybridization to the strands surrounding each hinge leads to transformational changes. Depending on the complementarity of the added ssDNA, folding can be triggered at the two hinges independently. This results in three distinguishable geometries (Fig. 1b): no-folding, a single-fold on either the left or the right 6HB, or two-folds on both left and right. Notably, single right or left folds cannot be differentiated using AFM or gel electrophoresis data.

Two types of folding mechanisms were engineered through DNA hybridization at the hinges. As a convention in this manuscript, complementary strands in all figures are denoted with the same color, and one of them is marked with a star (*). In the first mechanism (Fig. 1c), the input ssDNA consists of two segments (red*-green*) of functional sticky ends that are respectively complementary to the two sticky ends (red and green) on the two sides of the hinge. This input strand has 21-base functional sticky ends in each of the two segments, which are spaced by a neutral/non-functional 2-base T sequence. When the input ssDNA is presented to the circuit platform, it hybridizes with the two sticky ends on both sides of the hinge to fold the left two 6HB segments. After hybridization, the two 6HBs are tightly folded together between 0° and 60° of angle, slightly depending on factors like thermal fluctuations of the hinges, sticky ends design, AFM imaging properties, and the imperfectly rigid 6HB, etc. (See SI section 7 for discussion.) In the second type of folding mechanism (Fig. 1d), two different enable/input strands are required to complete the folding. The input magenta*-cyan is partially complementary to the left sticky ends (magenta) on the 6HB, and the input yellow*-cyan* is partially complementary to the right sticky ends (yellow). The cyan and cyan* segments of the

two input strands are complementary to eventually fold the right two 6HB. In all the experiments, the concentration of enable/input strands are ~ 50 nM, and the concentration of DNA origami, thereby the sticky ends on them, is ~ 0.5 nM. The ratio is $\sim 100:1$. (For details please see the method section.)

To close a hinge the hybridization energy must be greater than the bending energy of the hinge and the torque from the DNA force acting at points 14 nm from the hinge must be greater than the torque from the bending of the short single strands at the hinge vertex. We use a semi-flexible polymer model to obtain the bending force as a function of bending angles and rigidity. The bending energy is $E_B = K\theta^2/2$, where $K = \xi_p k_B T/L$ with ξ_p the persistence length and L as the rod length, which results in $E_B \sim 5k_B T$ and a maximum torque $\tau = 45$ pN-nm. These values are comfortably smaller than the hybridization energy for our 21-base sequence $\sim 30k_B T$ and a torque from the geometry and zipping force from hybridization of 112 pN-nm.

The tri-state output signals are read by the geometric changes of the 6HB trimer circuit platform. For the inputs we define the presence of the enable strand as “high”, and its absence as “low”. Similarly, the presence of the input strand is defined as “1”, and the absence of it as “0”. For the output signal, we define the no-folding linear geometry of the trimer (Fig. 1b) as “high impedance Z ”. One-fold, either on the left or on the right, is defined as output “0”. Two-folds, on both left and right, is defined as output “1”. We use AFM to directly visualize the three geometries. Due to the strong interactions between the DNA origami and the substrate during deposition, the geometry may vary slightly from its form in free solution. We also use electrophoretic gels to monitor the different geometries. Although the molecular weights of the trimer DNA rods are essentially the same the mobilities of the folded and straight configurations are significantly different. As we have previously seen in folded DNA structures [13], the folded geometry has lower mobility presumably because the hook-like fold readily latches onto the gel filaments and must untangle to proceed. As a result, the linear geometry passes through fastest while the two-fold geometry is the slowest.

To test the viability of our tri-state logic computation, we constructed a prototype for “AND” operation in two-state logic (Fig. 2a). For a short version of the logic gate platform, we make a dimer by connecting two 6HB DNA origami with a pair of functional sticky ends near the hinge (Fig. 2b). The two sticky ends (magenta and blue) are not complementary to each other, while respectively partially complementary to the two input strands, magenta*-green*

(input 1) and blue*-green (input 2). From the second type of folding mechanism, the folding is not activated until both input strands are present. In our experiment, output “0” is defined to be no-folding when both input 1 and input 2 are absent (0 and 0). The output remains “0” when input 1 is present (1) with input 2 absent (0), or when input 1 is absent (0) with input 2 present (1). The output returns signal “1”, which is designed to be a folded dimer, when both input 1 and input 2 are present (1 and 1). Characterized by both GEL (Fig. 2d) and AFM (Fig. 2e & 2f, S1 a-d), the two-state AND logic gate operates as designed.

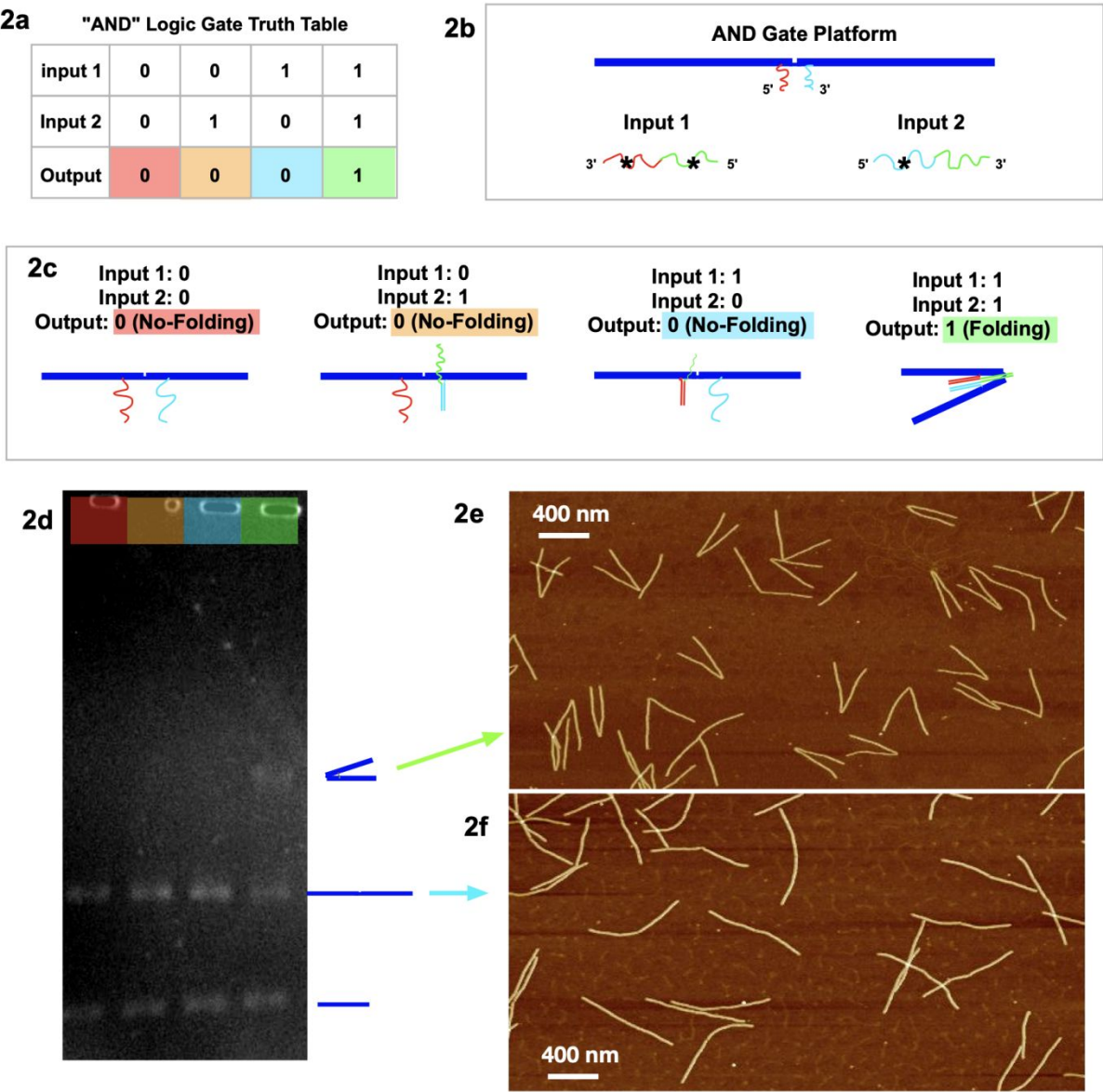


Figure 2. Design and data of logic gate “AND”. **a)** Truth table of “AND” logic gate of the DNA circuits. **b)** Design of the circuit platform with two input strands. **c)** Schematics of output signals in terms of no-folding/folding.

d) Agarose gel image of the four output signals with corresponding colors. The lowest band is 6HB monomer; the middle band is not folded (straight) 6HB dimer; the upper band is folded 6HB dimer. **e)** AFM images of folded dimer geometry with both input strands. Scale bar 400nm. **f)** AFM images of not folded dimer geometry.

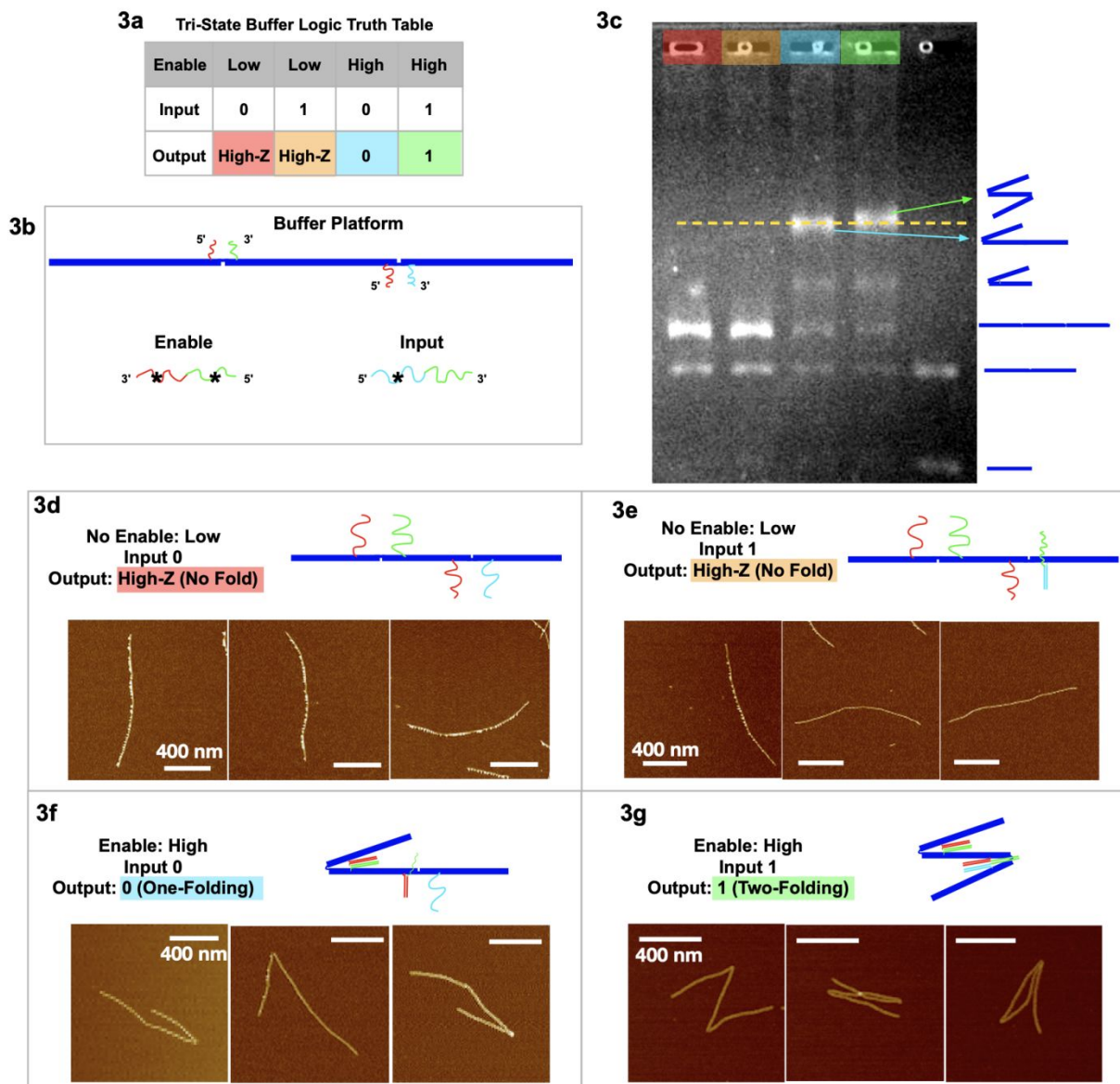


Figure 3. Tri-state logic gate, Buffer. **a)** Truth table. **b)** Schematics of the buffer tri-state DNA circuits platforms with input and enable strands. **c)** Agarose gel image of the four output signals with color headings corresponding to outputs in 3a, and a control sample lane with multiple geometries. **d)** AFM images of output high-Z (no-folding 6HB trimer geometry) with no enable or input strands. **e)** AFM images of output high-Z (no-folding geometry) with no enable but with input strand. **f)** AFM images of output 0 (one-fold) with enable but without input strand. **g)** AFM images of output 1 (two-folds) with both enable and input strands. AFM images scale bars 400nm. See Fig. S2 and S3 for statistics of global AFM.

Our two tri-state logic gates are illustrated in Fig. 3 (buffer) and Fig. 4 (inverter). For the tri-state buffer, the DNA origami platform with enable and input strands is detailed in Figure 3b. Note that the red sticky ends are identical on both hinges. When the enable strand is “low” (absence) and the input strand is “0” (absence), the trimer maintains the unfolded, linear geometry as “High-Z” (Fig. 3d). When the enable strand is “low” (absence) and the input strand is “1” (presence), the trimer remains unfolded “High-Z” (Fig. 3e), because the hybridization of the input strand on the right hinge does not activate any folding. When the enable strand is “high” (presence) and the input strand is “0” (absence), the left hinge is folded according to the first type of folding mechanism, however the right hinge is not folded with only one sticky end hybridized. This output is characterized as one-fold, signal “0” (Fig. 3f, S2). When the enable strand is “high” (presence) and the input strand is “1” (presence), both the hinges are folded according to the two types of folding mechanism, respectively (Fig. 3g, S3). With 2-folds the resulting output signal is “1”. In the two-folding (output 1) scenario, the extra input and enable should form a partial duplex stem with green-green* hybridized, leaving red* and cyan* single stranded. This red* on the partial duplex stem may have occupied the red sticky ends on the left hinge before a single-stranded enable would have hybridized at the hinge. However, the local concentration of sticky ends at the hinge is 10^5 times higher than the enable/input global concentration in the free solution, yielding more entropy gain for the green hinge sticky ends to displace off the partial duplex stem, to further fold the hinge. (See SI section 6 for detailed discussions.)

The gel image (Fig. 3c) shows four sample lanes (red, orange, cyan, and green) corresponding to the four output signals in the truth table (Fig. 3a), and a control (last lane) with multiple geometries. The gel shows that the two lanes with output 0 and 1 have the highest bands (indicating the slowest mobility structures), and we believe we may see a slight difference between the two. The green output “1”, with 2-folds, is more likely to entangle with the gel filaments and therefore migrates through porous gels slower than the blue output “0” with only 1-fold. It is interesting to note, folded dimers migrate slower than not folded (straight) trimers, even though the dimer has less molecular weight than the trimer. Some lanes have more bands resulting from leftover monomers not used to form dimer or trimer structures. The statistics of global AFM images (Fig. S2 & S3) have shown at least 70% of the targeted trimer folded accordingly in the buffer logic, excluding monomers, dimers, and non-specific aggregations.

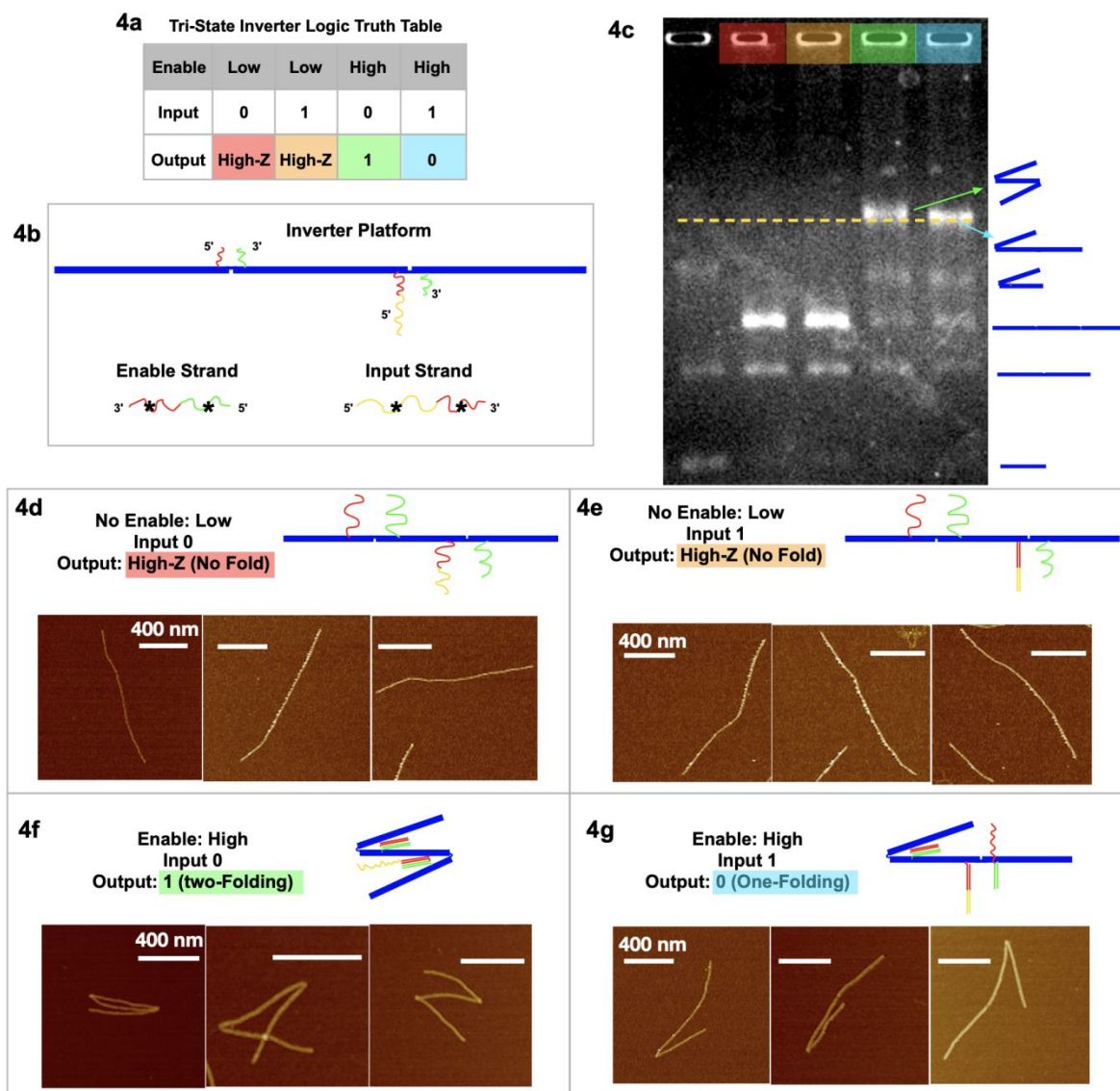


Figure 4. Tri-state logic gate, Inverter. **a)** Truth table. **b)** Schematics of the inverter tri-state DNA circuits platforms with input and enable strands. **c)** Agarose gel image of the four output signals in corresponding colors, and a control sample lane with multiple geometries. **d)** AFM images of output high-Z (no-folding 6HB trimer geometry) with no enable or input strands. **e)** AFM images of output high-Z (no-fold geometry) with no enable but with input strand. **f)** AFM images of output 1 (two-fold geometry) with enable but without input strand. **g)** AFM images of output 0 (one-fold geometry) with both enable and input strand. AFM images scale bars 400nm. See Fig. S4 and S5 for statistics of global AFM.

In the tri-state inverter logic gate (Fig. 4), the platform has been re-designed with functional sticky ends near the hinges with corresponding enable/input strands. Notably, the left sticky end on the right hinge now has two parts, red and yellow (Fig. 4c). When the enable strand

is “low” (absence) and the input strand is “0” (absence), the output is the no-folding linear geometry as “High-Z” (Fig. 4d). When the enable strand is “low” (absence) and the input strand is “1” (presence), the output remains no-folding “High-Z” (Fig. 4e). When the enable strand is “high” (presence) and the input strand is “0” (absence), the output returns signal “1” (two-folding), as the enable strand is able to bind at both hinges to fold the trimer twice (Fig. 4f, S5), according to the first type of folding mechanism. When the enable strand is “high” (presence) and the input strand is “1” (presence), the enable strand is only able to fold the left hinge but not the right hinge (Fig. 4g, S4), resulting in output “0” (one-folding). At the left hinge, there was another possibility that the red* on the input strand bound the red sticky ends, while the green* on the enable strand bound the green sticky ends. However, for the same argument of significantly (10^5 times) higher local concentration of sticky ends than the global concentration of the input/enable strands, the left hinge is preferred to bind to a same input strand for higher Gibbs Free Energy. The right hinge, on introducing the input strand, is unfolded by partially unzipping the red* part of the enable strand in the process of strand displacement. With only the enable strand present, the red-red* and green-green* segment are bound and the hinge closes. In the presence of both enable and input strands we have strand displacement; the input strand segment yellow* hybridizes with the hinge segment yellow and then continues hybridizing input red* with right hinge segment red displacing enable segment red*. The right hinge sticky ends are decoupled, and the hinge opens. This is (Gibbs free) energetically favored. The final state of the right hinge is hinge red-yellow hybridized to input red*-yellow*, hinge green hybridized to enable green*. We then have dsDNA red-yellow and dsDNA green, whereas before strand displacement we had dsDNA red and green. The net gain is the hybridization of the yellow segments. Again, we have obtained the statistics of global AFM images (Fig. S4 & S5) that shows at least 70% of the targeted trimer folded accordingly in the inverter logic, excluding monomers, dimers, and non-specific aggregations.

In conclusion, we have constructed DNA computation logic gates with DNA origami chains activated through DNA strand displacement. Our circuit gates can realize not only two-state Boolean logic, but tri-state logic as well, which is a novel addition to the DNA computation community. Our tri-state DNA circuits, both buffer and inverter gates, have been confirmed with gel electrophoresis and AFM imaging. Our work on DNA tri-state computation significantly

supplements Boolean logic with both research and industrial applications, using the biocompatibilities of DNA.

Methods

Tri-state logic DNA Origami Platform synthesis:

M13 scaffold strand and DNA staple strands were mixed at a ratio of 1:10 to anneal for 6HB DNA Origami monomer with a final concentration of 10 nM in 1×TAE 12.5 mM Mg²⁺ buffer. The temperature ramp was from 70 °C to 4 °C at 2 °C/hr. Then all six DNA origami monomers (3 for tri-state buffer and 3 for inverter platform design) after annealing individually were centrifuged to purify the extra staple strands at 2.2k RCF 4 times, with 15 mins each. The 1×TAE 12.5 Mg²⁺ buffer was refilled after each time of centrifugation. This is the same and only buffer for ALL our following experiments reported by this article. The three different 6HB DNA origami monomers were then mixed with ratio 1:1:1 to incubate at 42 °C for 3hrs, then ramped down to 20 °C at 2 °C/hr. (The accurate controlling of mixing ratio is key to obtain the high yield of the tri-state platform product.)

Adding input/enable strands to obtain output signals:

The tri-state buffer and inverter 6HB DNA origami trimer platforms were then applied to add input/enable strands accordingly to obtain different output signals. The ratio of concentration of origami platform to that of input/enable was 1:100, with a final concentration of origami, thereby the same concentration of sticky ends at the hinge, at 0.5 nM, and a final concentration of input/enable strands at 50 nM. Notably, in the cases where both input and enable strands were required, the two strands were added at the same time.

Reading Output Signals by Agarose Electrophoresis Gel:

The final products with different outputs were added in 0.8% agarose gel ran at room temperature at 50 V (relatively low to not incur significant temperature increase; Otherwise, over 50 °C in the gel may distort or damage the origami structures.) Then the gel was dyed with Ethidium Bromide for 10 mins, then washed with water for 3 mins before UV imaging.

Reading Output Signals by Atomic Force Microscopy

The final products with different outputs were also characterized by AFM by depositing diluted product solutions onto mica surface, followed by DI water rinsing and air pump drying for 3 times. The prepared samples on the mica were then imaged in air mode of the AFM.

Author Contributions

K. W., Q. H., M. E., B. K., P. C. and G. Z. contributed to initiation and management and performing and analyzing the experiments. K. W., P. C., and G. Z. contributed to designing the experiment, designing the DNA sequences and DNA origami.

Conflicts of Interest

We declare no conflicts of interest.

Acknowledgements

This research was primarily supported by U.S. Department of Energy (DOE) under grant DE-SC0007991 at NYU, (KW, QH, GZ, PMC) for designing the experiment, designing and synthesizing the DNA sequences and origami analyzing the data and writing the paper, and by Fairleigh Dickinson University (GZ, MRE, and BK) for performing the experiments and analyzing the data. We thank Ruojie Sha and Nadrian Seeman from the Department of Chemistry at New York University for meaningful discussions and technical support.

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