Long-distance electron transfer in a filamentous Gram-positive bacterium

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Long-distance extracellular electron transfer has been observed in Gram-negative bacteria and plays roles in both natural and engineering processes. The electron transfer can be mediated by conductive protein appendages (in short unicellular bacteria such as Geobacter species) or by conductive cell envelopes (in filamentous multicellular cable bacteria). Here we show that \textit{Lysinibacillus varians} GY32, a filamentous unicellular Gram-positive bacterium, is capable of bidirectional extracellular electron transfer. In microbial fuel cells, \textit{L. varians} can form centimetre-range conductive cellular networks and, when grown on graphite electrodes, the cells can reach a remarkable length of 1.08 mm. Atomic force microscopy and micro-electrode analyses suggest that the conductivity is linked to pili-like protein appendages. Our results show that long-distance electron transfer is not limited to Gram-negative bacteria.

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Electron transfer is essential for energy generation and the metabolism of life. Bacteria are versatile in their ability to transfer electrons to various chemicals and to preserve energy. In addition to respiration with intracellular chemicals such as oxygen, sulfate, or nitrate, bacteria can also respire with externally accessed chemicals such as mineral particles (i.e., extracellular electron transfer, EET).

Some single-celled bacteria are capable of long-distance electron transfer (LDET) to chemicals or other microbial cells at tens of micrometers distance and multicellular cable bacteria transport electrons in the range of centimetres.

Two bacterial LDET strategies have been identified: conductive protein nanowires generated by relatively short, unicellular bacteria (e.g., *Geobacter* species) and conductive envelopes formed by filamentous, multicellular cable bacteria. Conductive protein nanowires generated by *Geobacter* and several other microorganisms can transfer electrons over tens of micrometers.

These protein nanowires can form conductive networks and contribute to direct intercellular electron transfer in biofilms or aggregates composed of different microorganisms. Cable bacteria usually form centimetre long filaments as they consist of thousands of cells end-to-end to couple sulfide oxidation in anoxic sediment and oxygen reduction at the sediment surface in aquatic systems. The periplasmic fibers of cable bacteria have been shown to be conductive and can contribute to LDET. The wide occurrence of bacterial LDET networks affects microbial communities and biogeochemical processes in natural and engineered environments across the earth. All reported bacteria capable of LDET so far have been Gram-negative, and although Gram-positive bacteria are ubiquitous and some are capable of EET, they have not been expected to evolve LDET, as they possess very different cell surface layers.

Here, we report an additional bacterial LDET strategy represented by *Lysinibacillus varians* GY32, which is capable of bidirectional EET. In microbial fuel cells (MFCs) strain GY32 can form centimetre-range conductive cellular networks composed of insulated filamentous cells with conductive nanowire-like appendages.

**Results**

*L. varians* GY32 can form extremely long cells. Strain GY32 is a unicellular filamentous Gram-positive bacterium isolated from freshwater sediment and contains multiple nucleoids in each cell. Previously reported cell length of GY32 was up to about 500 μm with a uniform diameter (~0.5 μm) in nutrient-rich aerobic medium. In this study, we found that GY32 could grow into a longer shape when anaerobically respiring with graphite electrodes as the sole electron acceptor in MFCs (Fig. 1a and Supplementary Fig. 1). The longest GY32 cell observed in MFCs was 1.08 mm (Fig. 1a), which is longer than the two biggest unicellular bacteria reported before. Cell sections evidenced a single-cell structure of GY32 as no separation was noted that some multicellular bacteria, such as cable bacteria, can grow to centimetre lengths as they form chains of thousands of cells end-to-end to couple sulfoxide reduction at the sediment surface in aquatic systems. The periplasmic fibers of cable bacteria have been shown to be conductive and can contribute to LDET.

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**L. varians** GY32 can transfer electrons to graphite electrodes in both sediment and liquid environments. To test the possible EET capacity of strain GY32, sediment MFCs (SMFCs) were assembled in which the anode (graphite plate) can serve as a solid electron acceptor for microorganisms and the electricity can be used to evaluate the microbial EET rate in sediment (Fig. 2a, Supplementary Fig. 2). In the SMFCs containing sediment from the river where GY32 was isolated, the current density increased by 75.2 ± 7.1% after artificial inoculation of GY32 compared to those without GY32 supplement (2.8 ± 0.3 vs. 1.6 ± 0.1 μA/cm², Fig. 2b). A stable current could be maintained for over 10 days, indicating a relatively stable role of GY32 in the sedimentary microbial community. We also assembled SMFCs with sterilized sediments, where GY32 was supplemented to function as the only bacterium. This SMFC generated a current density of 0.9 ± 0.04 μA/cm², which was fivefold higher than that of rod-shape bacteria such as *Escherichia coli* (4.5 μm⁻¹) and much higher than that of big coccus *T. namibiensis* (0.004 μm⁻¹) and rod-shape *E. fisheloni* (0.05 μm⁻¹). A higher surface to volume ratio supports a faster rate of nutrient and waste exchange per unit of cell volume and thus a faster growth rate.
higher than that of the background electricity of the sterilized sediments (Supplementary Fig. 2). Live/dead bacteria staining showed that the filamentous GY32 were still alive in the sediments on day 20 after inoculation, and the cell density increased toward the anode surface (Supplementary Fig. 2). These results suggest that strain GY32 can grow in sediments through EET to solid electron acceptors as well as contribute to microbial EET processes in natural environments.

In MFCs containing defined liquid medium (Fig. 2c), GY32 could use acetate or formate as an electron donor for the reduction of graphite anode. In acetate-fueled MFCs, the maximum current density was $7.5 \pm 1.2 \, \mu A/cm^2$ after being incubated for 69 h (Fig. 2d). Moreover, the biomass of planktonic cells increased simultaneously with the acetate consumption and electricity generation (Supplementary Fig. 2E), suggesting that GY32 respired and grew with the anode as the sole electron acceptor. When respiring with anodes polarized at 0.4 V (vs. standard hydrogen electrode, SHE), strain GY32 generated a maximum current density of $11.7 \pm 1.1 \, \mu A/cm^2$ (Supplementary Fig. 2F). The current densities of MFCs catalyzed by L. varians GY32 were comparable with that of Shewanella oneidensis MR-1 using a graphite anode. Cyclic voltammetry curves of anodic GY32 biofilms showed an oxidative peak at 0.09 V and a reductive peak at $-0.08 \, \text{V vs. SHE}$ (Supplementary Fig. 2G) under non-turnover condition. A similar cyclic voltammetry profile with higher peak-current was observed in the presence of acetate as an electron donor (turnover condition), indicating redox species generated within biofilms.

We further tested the capability of L. varians GY32 using electrode as electron donor and Fe(III) citrate as electron acceptor in a biocathode electrochemical system (BCES, Fig. 2c). With a graphite cathode polarized at $-0.6 \, \text{V vs. SHE}$, GY32 showed a Fe(III) reduction rate of $8.9 \pm 1.1 \, \mu M/h$, while the polarized graphite cathode without GY32 showed a Fe(III) reduction rate of $2.9 \pm 0.5 \, \mu M/h$, and GY32 without the polarized cathode did not reduce Fe(III) (Fig. 2e). The possibility that $H_2$ was generated on the negatively polarized electrode and serves as an electron donor to Fe(III) reduction could be ruled out22,23 because no $H_2$ was accumulated in the cathode chamber ($H_2$ concentration maintained lower than $0.1 \, \mu M$, Fig. 2f) and L. varians GY32 cannot reduce Fe(III) even in the presence of $H_2$ (Supplementary Fig. 3). These results suggested that GY32 used the cathode as the sole electron donor to reduce Fe(III) in the BCESs. Moreover, L. varians GY32 could also use a polarized electrode (0.1 V vs. SHE) as an electron donor to reduce dissolved oxygen (Supplementary Fig. 4). Integrating with the electricity generating

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**Fig. 2 Bidirectional EET between GY32 and electrodes.** a Schematic of GY32 electricity generation in SMFCs. b Electricity generation by inoculating GY32 in SMFCs. c Schematic of GY32 EET in MFCs with liquid medium (upper reactor) and in BCESs (lower reactor). d Electricity generation by GY32 in MFCs with liquid medium. e Fe(III) reduction by GY32 with a cathode ($-0.6 \, \text{V vs. SHE}$) as the sole electron donor in BCESs. f $H_2$ concentration in the BCESs with or without GY32, inset shows the GY32 biofilms on the cathode. $n = 3$ for each experiment, plots show mean and standard deviation. Source data are provided as a Source Data file.
capabilities, our results showed that GY32 could behave as either electron donor or electron acceptor to extracellular redox particles. Such bidirectional EET capability of GY32 implies a possibility that GY32 could perform interspecies electron transfer with another bacterial cell. Moreover, since electron mediator synthesis would be hampered by the lack of a carbon source in the BCESs, it is more likely that GY32 received electrons from the cathode mainly by direct contact between the cells and the cathode surface.

*L. varians* and its appendages form conductive cellular networks. When transferring electrons to anodes in MFCs, the filamentous strain GY32 preferred to cluster and form network-like structures surrounding the anode surface (Fig. 3a, Supplementary Fig. 5). These networks could extend several centimetres from the anode surface into the liquid medium. The cell clusters developed unevenly on the anode surface, and most cells maintained the filamentous structure and high viability during electricity generation (Supplementary Fig. 5B). Figure 3a also showed that nanowire-like appendages along the filamentous cells formed subnetworks bridging different cells in the clusters. After being stained by Nano-Orange, a protein-specific fluorescent dye that has been used to visualize bacterial nanowires of *Geobacter* and *Shewanella* species, significant fluorescence was observed along with the cell-attached appendages, indicating that these are composed of protein (Fig. 3a).

The cell clusters from the cellular networks, consisting of GY32 cells and their appendages, were picked and used to connect two prefabricated gold electrodes with a 0.1 mm insulating (SiO₂) gap (Fig. 3b). When the voltage between the two electrodes was swept from −0.1 to 0.1 V, the current increased with the voltage (Fig. 3c).

When a fixed voltage of 0.1 V was applied, stable currents of 0.25 ± 0.06 nA were observed (Fig. 3d), suggesting an electronic conductance capability of the cell clusters. The calculated conductivity of GY32 cell clusters ranged from 0.1 to 0.2 mS cm⁻¹ (n = 18), depending on the structure and growth stage of GY32 cell clusters. This conductivity was in the range of the conductivity of *G. sulfurreducens* biofilms and mixed-species biofilms or microbial aggregates (from several to thousands of μS cm⁻¹). In contrast, control samples including (a) clusters of heat-killed GY32 cells, (b) clusters not connecting the gold electrodes, (c) culture supernatant showed much smaller responses to voltage. Moreover, the current obtained for the control samples at 0.1 V was one order of magnitude lower (0.01–0.04 nA) than that of the live GY32 cell clusters (Fig. 3c, d). The conductive GY32 cell clusters suggested that centimetre-range cellular networks around the anode were conductive. The cell clusters conductivity decreased when dried in air and could be recovered when rehydrated with deionized water, which was similar to *G. sulfurreducens* biofilms and consistent with a redox conductivity. Moreover, electrochemical gating measurements of biofilms grown on interdigitated microelectrode arrays (IMAs) showed a peak conductivity of 0.25 ± 0.1 mS cm⁻¹ at 0.05 V (vs. SHE) when the gate potential increased from −0.4 to 0.2 V (vs. SHE, Supplementary Fig. 6), which also suggested that the LDET of *L. varians* GY32 cellular networks is a redox process.

Kelvin probe force microscopy (KPFM) was then used to further understand the electrical properties of nanostructures in GY32 cell clusters. The samples were prepared on highly conductive gold-coated mica substrates and measurements were conducted using a two-pass lift mode. The first pass was used to probe the topography of the sample (Fig. 3e), and in the second pass, the probe was traced along with the sample at a certain height. A potential is applied between the probe and sample.
during the second pass to nullify interaction between the probe and sample in a frequency modulated feedback. The contact potential difference (also named surface potential) between the conductive tip and gold substrate was much smaller (5 ± 2 mV) than that between dried GY32 cell and gold substrate (53 ± 11 mV) (Fig. 3f, g). Unlike conductivity tests, KPFM does not produce a current flow but rather measures the long-ranged electrostatic interactions in the sample-probe capacitor set-up. The small potential difference between nanowire and gold showed a similar work function and could indicate that the appendages are much more conductive than the cell envelope of GY32.

Microelectrode tests suggested conductivity of GY32 appendages. The filamentous cells and their appendages are the main components in GY32 cellular networks. Based on the reported conductive cell envelope of cable bacteria and conductive nanowires of Geobacter species, the conductivity of both cell envelope and appendages of GY32 should be further evaluated. When we used a single GY32 cell (without appendages connecting the electrodes) to connect fabricated electrode arrays (Fig. 4a, b), no significant current was detected within a direct voltage of 0.1 V. Moreover, no obvious current was obtained when the voltage ranged from −0.1 to 0.1 V (Fig. 4c), regardless of using dried, wet, live or heat-killed cells, indicating that the GY32 cell envelope is not conductive. On the other hand, when electrodes on IMAs were connected by nanowire-like appendages extracted from GY32 cells (Fig. 4d, e), significant current (24.8 ± 4.0 pA, n = 8) was observed when a voltage of 0.1 V was applied between the electrodes, while the buffer showed only a current of 2.0 ± 0.5 pA. Similar to the GY32 cell clusters, the conductivity of appendages decreased when dried in air. These results strongly suggest that the appendages are conductive and can be responsible for the conductivity of the cell networks, although further study is needed to elucidate the chemical composition and electrical behavior of an individual appendage.

Possible components participating in the LDET of *L. varians* GY32. Dominant roles of Gram-positive bacteria have been evidenced in many microbial communities capable of reducing metal oxides or electrodes. EET strategies generally involve c-type cytochromes or electron shuttles, and EET has been observed for the Gram-positive bacteria *Enterococcus faecalis* and *Listeria monocytogenes* using flavins as electron shuttles. However, no available information was reported about nanowire-like appendages of Gram-positive bacteria in EET or LDET. The nanowire-like appendages of GY32 are too thin to be cell membrane extensions (10–150 nm) as found in *S. oneidensis* MR-1 or flagella (15–20 nm). The appendages of GY32 have a similar size to the conductive type IV pili of some Gram-negative bacteria (i.e., e-pili). In the genome of *L. varians* GY32 (accession number NZ_CP006837.1, https://www.ncbi.nlm.nih.gov/nuccore/NZ_CP006837.1), gene T479_RS14015 (https://www.ncbi.nlm.nih.gov/nuccore/754147054) is predicted to encode ComGD, a putative type IV pilin. The high density of aromatic amino acids is considered to be a key property in
conductive type IV pili and arachellum. The percentage of aromatic amino acids in GY32-ComGD is 13.8% (19/137 amino acids, Supplementary Fig. 7), which is comparable or even higher than that of tested conductive pili. The largest gap between those aromatic amino acids is 24 amino acids, also smaller than the suggested upper limit of 35 amino acids. In addition, three key amino acids are usually considered in e-pili, a phenylalanine (F1) initiating the a-helix domain, a glutamic acid residue in position +5 (E5), and a tyrosine at position +57 (Y57, catalyzing electron transfer to extracellular electron acceptors). Consistently, cytochrome-fl types of microbial LDET networks have been intensively studied. Although important environmental roles and promising applications of bacterial protein nanowires have been reported, the compositions and mechanisms of many of these nanostructures are still unclear.

Discussion

Here, we have shown that the unicellular bacterium \textit{L. varians} GY32 is capable of bidirectional EET and can form centimetre-scale conductive cellular networks, growing into remarkably long cells when anaerobically respiring with graphite electrodes as the sole electron acceptor.

Gram-positive bacteria are ubiquitous in various environments and can be dominant in some iron- or electrode-reducing bacterial–metal interfaces. Centimetre-long cell networks of GY32 can form around the solid electron acceptors (Fig. 3a). Given that GY32 is a facultative anaerobic bacterium, it might potentially form conductive networks in both oxic and anoxic environments.

**Methods**

**Bacterial culture.** \textit{L. varians} GY32 was isolated from heavy metals-polluted sediment and preserved in our laboratory. Strain GY32 was cultivated aerobically in Luria–Bertani broth (LB) for 12 h (30 °C, 120 rpm) in flasks. The LB (1 L) contained 5 g yeast extract (LP0021, Oxoid, United Kingdom), 10 g Tryptone (LP0042, Oxoid, United Kingdom), and 5 g NaCl. Before being used for inoculation to MFCs or further tests, the LB-cultivated bacteria cells were washed in sterilized phosphate buffered saline (PBS) or deionized water for at least three times by centrifugation at 8000×g for 5 min. PBS used here (pH 7.2, 1 L) contained 8 g NaCl (C111545, Aladdin, China), 0.2 g KCl (P112133, Aladdin, China), 0.36 g Na₂HPO₄·12H₂O (S112623, Aladdin, China), 0.24 g KH₂PO₄ (P104071, Aladdin, China), and 5 mM of formate (S164504, Aladdin, China) or acetate (S118649, Aladdin, China) as the sole electron donor. PBS supplemented with 50 mM potassium ferricyanide (C01512028, Macklin, China) was used as catholyte. The pH was adjusted by HCl (10011008, Hushi, China).

**Nanowire appendage preparation.** Nanowire-like appendages were extracted following the methods reported before. Briefly, planktonic cells were harvested from MFCs and preserved in 2 ml dialyzed ethanolamine buffer and stored under 4 °C before microscoopic and conductivity tests. The ammonium sulfate \((\text{NH}_4\text{SO}_4)\) and ethanolamine \((\text{HBO}_2)\) used as catholyte. The anode culture was inoculated with the PBS-washed \textit{L. varians} cells with an initial OD₅₆₀ of 0.02. The anode chambers of the MFCs were bubbled with pure \(\text{N}_2\) until...
the dissolved oxygen in the medium was below 0.3 µM with an oxygen micro-electrode (detection limit: 0.3 µM, OX-14125, Unisense, Denmark). Titanium wire with a diameter of 20 µm was used to construct the cathode and anodes in each MFC and the voltage of the resistor was recorded with a multimeter (Keithley 2700, USA) to calculate the current. MFCs were operated under 30 °C. The MFC setup is illustrated in Fig. 2c. Anodic bacterial growth was determined by quantifying the dissolved oxygen in the medium was below 0.3 µM with an oxygen micro-electrode (ox210, Unisense, Denmark). To further test the EET capability of L. varians GY32 to a polarized electrode, cyclic voltammetry and electrochemical gate measurements were performed with a probe station equipped with a Keithley 2614B source meter in an ambient environment (25 °C). In addition to cell clusters, control samples including uncentrifuged bacteria culture, culture supernatant, heat-killed cells, and deionized water were also tested. A voltage, typically ranged from 0.1 to 0.1 V, was applied between the two gold electrodes to test the conductivity of the individual cells, 2 µL of a cell suspension containing bacteria culture or the nanowire appendages extracted from GY32 culture. A microelectrode buffer containing nanowire appendages (n = 4), or ethanolamine buffer without nanowire appendages as a control, was loaded on an electrode array. The electrode array was then observed with AFM to confirm the connection of electrodes by nanowires (Fig. 4e). The I−V (from −0.1 to 0.1 V, scan rate 10 mV/s) and I-t (0.1 V maintained for 200 s) profiles of the electrode array connected by these cells were tested (from 0 to 0.1 V, scan rate 2 mV/s). 

**BCEs assembly and operation.** Three dual-channel BCEs were assembled as previously reported. Graphite plates (2 x 3 x 0.1 cm, Koboi, China) connected to titanium wires were used for both anodes and cathodes. For cathodic Fe(III) reduction, both cathode and anode chamber contained 100 mL sterilized PBS. The cathode chamber was supplemented with GY32 (washed for three times with sterilized PBS and the dissolved oxygen was 233.8 ± 2.7 µM) and the dissolved oxygen was 233.8 ± 2.7 µM. Similarly, three dual-channel BCEs containing sterilized sediments inoculated with strain GY32 and 10 mM of formate, three SMFCs containing sterilized sediments were tested. After being air-dried, the samples were loaded on a prefabricated electrode array with 1 mm wide gold electrodes separated by 0.1 mm insulating SiO2-gaps. The DC measurements through the fully hydrated cell clusters were performed with a probe station equipped with a Keithley 2614B source meter in an ambient environment (25 °C). In addition to cell clusters, control samples including uncentrifuged bacteria culture, culture supernatant, heat-killed cells, and deionized water were also tested. A voltage, typically ranged from 0.1 to 0.1 V, was applied between the two gold electrodes to test the I−V profiles of different samples with a scan rate of 10 mV/s. I-t profiles of the samples at a voltage of 0.1 V maintained for 200 s were further processed and analyzed by NanoSpec Analysis 1.9 (Bruker, USA). KPFM mode was used to measure the surface potential of GY32 cell clusters, cell clusters (n = 18 different bacterial cultures) were picked from the MFC cultures with a glass hook and then washed with deionized water five times. After being air-dried, the samples were scanned with a lift scan height of 50 nm and a drive amplitude of 2 V. The AFM investigation was performed for three independent cultures of L. varians GY32 all showing similar results.

**Direct current (DC) conductivity tests via electrode arrays.** The conductivity of cell clusters and nanowires was tested under fully hydrated conditions. To test the conductivity of the cell clusters, cell clusters (n = 18 different bacterial cultures) were picked from the MFC cultures with a glass hook and then washed with deionized water five times. The clusters were then loaded on a prefabricated electrode array with 1 mm wide gold electrodes separated by 0.1 mm insulating SiO2-gaps. The DC measurements through the fully hydrated cell clusters were performed with a probe station equipped with a Keithley 2614B source meter in an ambient environment (25 °C). In addition to cell clusters, control samples including uncentrifuged bacteria culture, culture supernatant, heat-killed cells, and deionized water were also tested. A voltage, typically ranged from 0.1 to 0.1 V, was applied between the two gold electrodes to test the I−V profiles of different samples with a scan rate of 10 mV/s. I-t profiles of the samples at a voltage of 0.1 V maintained for 200 s were further processed and analyzed by NanoSpec Analysis 1.9 (Bruker, USA). KPFM mode was used to measure the surface potential of GY32 cell clusters, cell clusters (n = 18 different bacterial cultures) were picked from the MFC cultures with a glass hook and then washed with deionized water five times. After being air-dried, the samples were scanned with a lift scan height of 50 nm and a drive amplitude of 2 V. The AFM investigation was performed for three independent cultures of L. varians GY32 all showing similar results.

**Cyclic voltammetry and electrochemical gate measurements.** After the tests of the current generation by GY32 with 0.4 V polarized anodes, cyclic voltammetry profiles of GY32 biosfilms on working electrodes were measured under turnover conditions (with acetic acid as electron donor). Before the test, three MFCs were replaced with anarobic (N2-bubbled) fresh PBS while the anodic GY32 biosfilms and Ag/AgCl reference electrodes were maintained and non-turnover cyclic voltammetry profiles were recorded. During cyclic voltammetry measurements, the anode potential varied between −0.4 and 0.3 V (vs. SHE) with a scan rate of 2 mV/s. The current generation by GY32 was also tested. The cyclic voltammetry of bare electrodes in anarobic PBS was also tested to evaluate the background current.

**Electrochemical gating measurements of GY32 biosfilms were conducted using a bipotentiostat model of Autolab PGSTAT322N electrochemical workstation (Metrohm, Switzerland), as described before.** Biological L. varians GY32 were grown on IMAs (Yuxin, China) serving as anodes in MFCs. The IMAs consisted of 50 parallel gold rectangular bands, each 2 mm long × 20 µm wide × 100 nm thick, with 20 µm gaps patterned onto a SiO2 substrate. The two ends of IMAs were connected to Ti-wires via silver pastes (Electrolub, United Kingdom). Biosfilms grown on IMAs in aerobic LB medium (30 °C for 24 h) were observed under a microscope to ensure the separated electrode arrays were connected by biosfilms. Biosfilms-connected IMAs and Pt-wires were then used as working electrode and counter electrode, respectively, in glass bottles containing 100 mL of anaerobic PBS (at 30 °C). One microliter buffer containing nanowire appendages (n = 4), or ethanolamine buffer without nanowire appendages as a control, was loaded on an electrode array. The electrode array was then observed with AFM to confirm the connection of electrodes by nanowires (Fig. 4e). The I−V (from −0.1 to 0.1 V, scan rate 10 mV/s) and I-t (0.1 V maintained for 200 s) profiles of the electrode array connected by these cells were tested. To test the conductivity of the individual cells, 2 µL of GY32 culture, after being diluted by 1000-fold with deionized water, were loaded on a laboratory fabricated electrode array (Fig. 4b). Cells (n = 5) connecting two or more electrodes were located under an optical microscope and the I−V profile between the electrodes connected by these cells were tested (from −0.1 to 0.1 V, scan rate 2 mV/s) with the probe station equipped with a Keithley 2614B source meter in the ambient environment (25 °C).
The transcriptome data that support the findings of this study have been deposited in the Gene Expression Omnibus with accession number GSE165753. Source data are provided with this paper.

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Author contributions

MX., L.P.N., and M.D. conceived and supervised the project. Z.W., Y.Y., R.B., M.M., and J.M. carried out experiments including nanowire and bacteria cell conductivity tests. Y.Y., G.S., J.G., and Y.M. carried out the bacteria cultivation and CLSM observation. L.H.K., C.G., and D.L. conducted the AFM measurements. Y.Y., G.K., D.L., J.T.B., and C.G. performed MFC and MES experiments and data analysis. G.K. and C.Z. analyzed the genome sequence and gene expression data. All authors discussed the results. Y.Y., L.H.K., and M.D. performed data analysis and wrote the paper with comments from all the other authors.

Competing interests

The authors declare no competing interests.

Additional information

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