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Supplementary Information 1. Theoretical Background

An ionic gradient across a selectively permeable membrane gives rise to an electromotive force across that membrane. This phenomenon can be described and modeled as follows:

The Nernst-Planck equation (Equation S1) defines the flux of ion *s* in an electric field.

$$J_s = -D_s\left[\nabla c_s + \frac{Fz_s}{RT}c_s\nabla\varphi\right] \quad \text{(S1)}$$

J_s (mol m^{-2} s^{-1}) is the molar flux of ion *s*, D_s (m^2 s^{-1}) is the diffusion coefficient of *s* in its medium, c_s (mol m^{-3}) is the molar concentration of *s*, F (C mol^{-1}) is Faraday's constant, z_s is the charge of *s*, R (J mol^{-1} K^{-1}) is the gas constant, T (K) is the temperature, and φ (V) is the electrical potential. In the 1940s, Goldman, Hodgkin, and Katz formulated a version of this equation for considering electric currents in biological membrane systems by making the assumptions that the membrane behaves as a homogeneous medium, that the electric field is constant throughout the membrane, and that fluxes of ions are independent of one another[1–4]. Equation S2 shows the resulting Goldman-Hodgkin-Katz (GHK) current equation.

$$I_s = P_s V F^2 z_s^2 \frac{[\mathrm{S}]_i - [\mathrm{S}]_o e^{-VFz_s/RT}}{RT\,(1-e^{-VFz_s/RT})} \quad \text{(S2)}$$

I_s (A m^{-2}) is the current density carried by *s* across the membrane, P_s (m s^{-1}) is the permeability of *s* through the membrane, V (V) is the voltage across the membrane, and $[\mathrm{S}]_i$ and $[\mathrm{S}]_o$ (mol m^{-3}) are the concentrations of *s* inside and outside the cell. Sodium, potassium, and chloride are the three ions most relevant to the study of excitable membranes. When formulated to consider the total ionic current density I (A m^{-2}) from the combined flux of

these three ions, the GHK current equation appears as Equation S3.[2]

$$I = \frac{VF^2\left[(P_{Na}[\mathrm{Na^+}]_i + P_K[\mathrm{K^+}]_i + P_{Cl}[\mathrm{Cl^-}]_o) - (P_{Na}[\mathrm{Na^+}]_o + P_K[\mathrm{K^+}]_o + P_{Cl}[\mathrm{Cl^-}]_i)e^{-VF/RT}\right]}{RT(1-e^{-VF/RT})} \quad \text{(S3)}$$

At open circuit (I = 0), Equation S3 reduces to the GHK voltage equation (Equation S4).[2]

$$V_{OC} = \frac{RT}{F}\ln\left(\frac{P_{Na}[\mathrm{Na^+}]_o + P_K[\mathrm{K^+}]_o + P_{Cl}[\mathrm{Cl^-}]_i}{P_{Na}[\mathrm{Na^+}]_i + P_K[\mathrm{K^+}]_i + P_{Cl}[\mathrm{Cl^-}]_o}\right) \quad \text{(S4)}$$

V_{OC} (V) is the open-circuit or zero-current voltage across the membrane. (By the convention used here, positive membrane potentials indicate that the interior of the cell is positive with respect to the exterior; note that this is the opposite of the convention used by Hodgkin and Katz.[2]) If the membrane is completely nonselective (i.e. $P_{Na} = P_K = P_{Cl}$) or no concentration gradient exists ($[S]_i = [S]_o$ for all species s), no voltage will arise.

Increasing the ratio of the ion permeabilities or the concentration gradient between compartments increases the voltage across the membrane. On the other hand, increasing the magnitude of the membrane's *absolute* permeability to the ions will increase the ionic current through the membrane. Permselectivity and absolute permeability are therefore critical parameters that define the power characteristics of this type of membrane system. A discussion of how to determine these parameters follows.

In a membrane system containing only two ions with sufficiently high concentrations and membrane permeances to impact the electrochemical environment, the third ion can be disregarded and removed from this equation on the basis of having negligible concentration

or permeability. Subsequently, the ratio of the membrane's permeability to each of the two relevant ions can easily be determined from the open-circuit voltage and species concentrations. Equation S5 considers sodium and potassium, the two most permeant ions in the electrocytes of *Electrophorus electricus* (multiple reports indicate that chloride conductance is minimal by comparison[5–7]).

$$\frac{P_{Na}}{P_K} = \frac{[\mathrm{K^+}]_i \, e^{V_{OC}F/RT} - [\mathrm{K^+}]_o}{[\mathrm{Na^+}]_o - [\mathrm{Na^+}]_i \, e^{V_{OC}F/RT}} \tag{S5}$$

In the electric eel, electrocyte interiors contain high concentrations of potassium (150 mM) and low concentrations of sodium (5 mM); the extracellular compartments contain high concentrations of sodium (160 mM) and low concentrations of potassium (2.5 mM). The resting potential of the membranes is -85 mV, reflecting the membrane's open K^+-selective channels in the resting state[8,9]. As described in the main text, in the posterior electrocyte membrane these K^+ channels close and voltage-gated Na^+ channels open in response to a neural impulse; these changes comprise a sudden modulation of P_{Na} and P_K that triggers the reversal of the membrane voltage to +65 mV at its peak[8–10]. **Extended Data Table 1** shows the permeability ratios of the posterior electrocyte membrane in the resting state and at the peak of an impulse. The anterior membrane displays no electrical excitability and constantly maintains the resting permeability ratio.

Equation S6 considers sodium and chloride, the two mobile ions present in the tetrameric hydrogel cells presented here:

$$\frac{P_{Na}}{P_{Cl}} = \frac{[\mathrm{Cl^-}]_o \, e^{V_{OC}F/RT} - [\mathrm{Cl^-}]_i}{[\mathrm{Na^+}]_o - [\mathrm{Na^+}]_i \, e^{V_{OC}F/RT}} \tag{S6}$$

Fixed charges in ion exchange membranes cause those membranes to be quite permeable to oppositely-charged counter-ions while rejecting co-ions of the same charge sign, a principle

known as Donnan exclusion[11]. Likewise, including charged monomers (**Extended Data Fig. 1**) imparted charge-based ionic selectivity to the hydrogels considered in this work. Measuring the open-circuit voltage across the cation- and anion-selective hydrogels used here in the presence of a salinity gradient yielded each gel's permeability ratio according to Equation S6 (**Extended Data Table 1**). The strategy of creating additive potentials by separating alternating fresh-water and saline reservoirs with alternating cation- and anion-selective membranes is known as reverse electrodialysis; flow systems using this arrangement are an emerging alternative energy technology for extracting electrical power from naturally-occurring salinity gradients.[12–16]

Calculating the *absolute* permeability of a membrane to an ionic species from an electrical recording requires the use of the GHK current equation. If a full current-voltage relation for a membrane is known (as with the artificial organ presented here), it can be fit directly to Equation S3[2,10]; absolute permeabilities of selective gels calculated in this way are shown in **Extended Data Table 2**. Alternatively, a first approximation can be obtained from electrophysiology literature using Equation S7, first reported by Hodgkin and Katz in 1949:

$$G = \frac{V_{OC}F^3}{R^2T^2}\left[\frac{(P_{Na}[\mathrm{Na}^+]_o+P_K[\mathrm{K}^+]_o+P_{Cl}[\mathrm{Cl}^-]_i)(P_{Na}[\mathrm{Na}^+]_i+P_K[\mathrm{K}^+]_i+P_{Cl}[\mathrm{Cl}^-]_o)}{(P_{Na}[\mathrm{Na}^+]_o+P_K[\mathrm{K}^+]_o+P_{Cl}[\mathrm{Cl}^-]_i)-(P_{Na}[\mathrm{Na}^+]_i+P_K[\mathrm{K}^+]_i+P_{Cl}[\mathrm{Cl}^-]_o)}\right] \quad \text{(S7)}$$

where G (Ω^{-1} m^{-2}) is the membrane's area-normalized conductance, defined as $(dI/dV)_{I\to 0}$. In the context of electrocytes with negligible chloride flux, this relationship can be reformulated as Equation S8. If the open-circuit voltage and ion concentrations are known, the permeability ratio can be calculated as in Equation S5, making the absolute permeability of both ions accessible.

$$P_{Na} = \frac{R^2T^2G}{F^3V_{OC}}\left[\frac{\left([\mathrm{Na^+}]_o+\frac{P_K}{P_{Na}}[\mathrm{K^+}]_o\right)-\left([\mathrm{Na^+}]_i+\frac{P_K}{P_{Na}}[\mathrm{K^+}]_i\right)}{\left([\mathrm{Na^+}]_o+\frac{P_K}{P_{Na}}[\mathrm{K^+}]_o\right)\left([\mathrm{Na^+}]_i+\frac{P_K}{P_{Na}}[\mathrm{K^+}]_i\right)}\right] \quad \text{(S8)}$$

Approximate values for the absolute ion permeabilities of the posterior, innervated membrane in its firing state that we calculated in this way from data reported by Shenkel and Sigworth[10] appear in **Extended Data Table 3**. Unfortunately, many of the other published data sets from *Electrophorus* were collected across whole cells rather than individual membranes[17], did not report normalization factors such as area required to approximate current-voltage relations or conductances[18,19], or focused on conductances at timepoints after the peak to study phenomena such as K^+ channel inactivation[19,20], limiting the number of data sets that we could use in this comparison. Further, early voltage-clamp setups were likely plagued by leak current pathways[8,21] (as detailed in [10]), as measured membrane resistances increased significantly with the advent of modern patch-clamp technique[10]. The assumptions required for the calculations appear in the footnotes of the table; accordingly, these values should be taken as a first approximation. A rare reported absolute P_{Na} value (3.4×10^{-7} m s^{-1} for experiment 8179b.1a in Shenkel and Sigworth's Table 1, reported on that paper's p. 1018[10]) confirms the validity of our assumptions, as the corresponding P_{Na} for that experiment calculated from the parameters reported in that paper's Table 1 is 3.6×10^{-7} m s^{-1}.

Ionic permeabilities and their ratios are important parameters of membranes in energetic contexts because they determine a membrane's power characteristics. Practically speaking, however, the power characteristics are more easily determined directly. We present a discussion of the internal resistance R_{int} and the maximum power density D_{max}, the two parameters most relevant to a membrane system's ability to generate electrical power, in **Supplementary Information 4**.

Supplementary Information 2. Dissipation experiments at open circuit

When an ionic gradient exists across a permselective membrane at open circuit, the gradient dissipates at a rate limited by the flux of that membrane's non-favored ion (e.g. the flux of Na^+ across an anion-selective membrane) and osmotic effects even in the absence of a connected load[13,22]. In the artificial electric organ, this gradient dissipation is avoided when the gels are kept out of contact with one another. In the electric eel, the gradients are maintained via active transport by the Na^+/K^+-ATPase[9,23].

In order to quantify the dissipation rate of the gradients in the tetrameric hydrogel cells, we pipetted 500 μL of each gel cell component onto a single substrate and cured the solutions for 90 seconds at a distance of 12 mm, forming gel disks (diameter = 1.9 cm, height = 0.2 cm). We peeled off the gels from the substrate and placed them in a custom-built Teflon chamber which allowed us to maintain a constant force of approximately 2.2 N on our cell perpendicular to the gel-gel interfaces. We recorded the voltage across the cell in the absence of any connected load for over 12 hours. We performed one experiment open to air and one experiment in which the gel cell was completely submerged in mineral oil. Traces of voltage over time are shown in **Extended Data Figure 2**.

Supplementary Information 3. Discharging and recharging the artificial electric organ

We pipetted 500 μL of each gel cell component onto a single substrate and inserted spiral Ag/AgCl wire electrodes into both of the high-salinity reservoir solutions. We then cured the solutions for 2 min at a distance of 12 mm, forming gel disks (diameter = 1.9 cm, height = 0.2 cm). We peeled the gels off of the substrate and placed them in the Teflon chamber (**Supplementary Information 2**), and maintained a constant force through the cell of approximately 2.2 N during the discharge-recharge cycles. At the beginning of each cycle, the cell was discharged in short circuit conditions for 15 min while recording the current

through the cell. We then recharged the cell with a 1 mA current for 2 min. We repeated this procedure for 10 cycles and integrated the current traces over time to calculate the capacity of the cell during each discharge. The discharge capacity (the current integrated over time during a discharge) remained above 90% of the initial discharge after ten such cycles (**Extended Data Fig. 3**).

Supplementary Information 4. Calculation of maximum power density of a stack of selective membranes

Electrophorus' electrocytes at the peak of a discharge and the hydrogel cells of the artificial electric organ are each systems that behave approximately ohmically, which is to say that the internal resistance (R_{int}) of each system is practically independent of the load resistance (R_{load}) (see **Extended Data Fig. 6**). This behavior is characterized by linear current-voltage relations as seen in **Fig. 2c,f** in the main text for gel cell systems and throughout the electrophysiology literature for *Electrophorus*[8,10,17,24] (in papers using the voltage-clamp strategy, the quadrant of interest is often reported as having positive voltage and negative current[8,10]). This line's intercept on the voltage axis is the open-circuit voltage V_{OC} (V), the intercept on the current axis is the short-circuit current I_{sc} (A), and the slope is the internal resistance R_{int} (Ω); the three parameters are related by Ohm's law referring to a circuit where R_{load} is zero (Equation S9).

$$R_{int} = -\frac{V_{OC}}{I_{sc}} \tag{S9}$$

It should be noted that when current conduction occurs through an ionic pathway, $R_{int} = \rho\frac{l}{A}$, where ρ is the resistivity (Ω m, a material property), l is the length, and A is the cross-sectional area. The maximum power of an ionic pathway is therefore directly

proportional to the cross-sectional area of that pathway and inversely proportional to its length. Maximizing the area while minimizing the length is therefore advantageous to a system's power characteristics; the ideal geometry resembles a stack of thin films. It should also be noted that the resistance of the hydrogel cell system is dominated by the reservoir gel containing the lower electrolyte concentration (0.015 M), whose resistivity is approximately 125 Ω m.

When the artificial electric organ is connected over a load,

$$P = V_{load} I = \frac{{V_{load}}^2}{R_{load}} \tag{S10}$$

where P is the power output (W, not counting power lost to the internal resistance), I is the current through the circuit, R_{load} is the load resistance (Ω), and V_{load} is the voltage across R_{load} (V).

According to the maximum power transfer theorem, maximum power output P_{max} (W) is obtained when $R_{load} = R_{int}$, the tetrameric gel cell's internal resistance (Ω). With a linear current-voltage relation, $V_{load} = V_{OC}/2$ under this condition, so

$$P_{max} = \frac{{V_{OC}}^2}{4R_{int}}. \tag{S11}$$

In the systems considered here, $V_{OC} = n * V_{OC,cell}$ where n is the number of tetrameric gel cells in the system and $V_{OC,cell}$ is the open-circuit voltage of a single tetrameric gel cell. Likewise, $R_{int} = n * R_{int,cell}$. As a result,

$$P_{max} = \frac{{V_{OC,cell}}^2 * n}{4R_{int,cell}} \tag{S12}$$

To obtain the maximum power density D_{max} (W m^{-2} $cell^{-1}$), P must be divided by the total gel area and the number of tetrameric gel cells stacked in series. If A is the cross-sectional area of the stack (m^2) and there are four gels per cell, then:

$$D_{max} = \frac{P_{max}}{n*A} = \frac{{V_{OC,cell}}^2}{4*A*R_{int,cell}}. \quad \text{(S13)}$$

In the case of our 80˚ *Miura-ori* example, $V_{OC,cell}$ = 0.170 ± 0.004 V, A = 0.866 cm^2, and $R_{int,cell}$ = 6.9 kΩ, so D_{max} = 0.027 ± 0.002 W m^{-2} $cell^{-1}$. This figure is presented alongside power densities calculated for *Electrophorus*' electrocytes in live eels in **Table 1** in the main text.

Supplementary Information 5. The 45˚ *Miura-ori* fold as a printable non-planar gel arrangement

In addition to the 80˚ *Miura-ori* fold presented in the main text, which required ionic conduction through holes in the substrate, we developed a printable gel cell geometry using another characteristic angle of the *Miura-ori* fold. Tesselating parallelograms with an acute angle of 45˚ form a sheet that can be folded into "mountains" and "valleys;" when compressed, the panels in the parallel valleys come into contact in a sequential series, each panel touching only the panel in front of it and the panel behind it in the series (**Extended Data Fig. 4**). This geometry is amenable to patterning, as gels need only be patterned on one face of the substrate to come into contact in series (and parallel) upon folding. We printed diamond-shaped gel patterns onto the panels of laser-cut sheets before folding them (see Materials and Methods). The 45˚ fold represents a robust, printable geometry in which an arbitrary number of parallel series of arbitrary numbers of gel cells can be patterned and

automatically brought into aligned contact by manipulating one degree of mechanical freedom. However, its utility in terms of improving the maximum power output of the artificial electric organ is limited, as there is invariably a degree of lateral conduction that scales with the length of a series. When comparing a 45˚-folded artificial electric organ with a lateral analogue with panels of identical dimensions, we found that the power output was nearly identical. We attribute this to a similar lateral conduction distance through the low-salinity gel, which provides the highest resistance in the system (**Extended Data Fig. 5**).

The gel precursor solutions were the same as in the printed artificial electric organ. We printed each of the gel precursors onto a single substrate that had been laser-cut with perforations in the Miura-ori pattern (45°; short edge of parallelogram = 3 cm, long edge = 4.24 cm) and corner holes corresponding to the size and position of pillars on the print plate for repeatable alignment. Before gel printing, we first printed P100 hydrophilic solution inside the parallelograms such that the hydrophilic coat ended approximately 1 mm from each perforation. We subsequently filled these parallelograms with the four gel precursor solutions using the printer (**Video 2**). The solutions were cured under the UV lamp (302 nm) at a distance of 12 mm and the substrate was folded into contact (**Extended Data Fig. 4**).

Supplementary Information 6. Impedance characterization of tetrameric gel cells

We have characterized the components opposing the flow of ionic current within a tetrameric gel cell. Porous, hydrated polymer membranes containing fixed charges that impart permselectivity via Donnan exclusion (see **Supplementary Information 1**) have previously been modeled as R(RQ)(RQ) impedances[25–27]. In other words, each membrane can be considered as a series arrangement containing a purely resistive component (R) attributed to the membrane itself and one or more parallel arrangements of a resistance and an imperfect

capacitance (Q) attributed to double layer and boundary layer effects in an electrolyte solution. The resistance of each component of a membrane's impedance is strongly dependent on the ionic strength of the solutions that surround it[26,27]. In order to assign the resistances of the membrane gels in the artificial electric organ, we therefore performed measurements on the membranes as they appear in tetrameric gel cells: separating compartments of low and high salinity.

We programmed a Metrohm Autolab PGSTAT302N in galvanostatic mode to collect time-courses of measurements that alternated between DC current-voltage relations and AC electrical impedance spectra (sweeping from 1 MHz to 10 Hz). We used a four-electrode setup; the working and counter electrodes were 2-cm coils of platinum wire (Sigma), while voltages were measured by Ag/AgCl wire electrodes prepared via the bleach method and curled into 2-cm coils. The compositions of the gels used were the same as in the printed artificial electric organ (Methods); we performed measurements on stacks of gel discs 18 mm in diameter and 1.8 mm thick in a Teflon chamber (**Supplementary Information 2**) while applying a constant force of approximately 2.2 N. Each electrode was embedded in a high-salinity gel in order to minimize the contribution of electrode placement and chloride offset between the two voltage-measuring electrodes. The gel/electrode assembly was inside a Faraday cage during all experiments.

We determined DC resistances by calculating the slope of the *I-V* curves. The AC impedance of each setup had a negligible imaginary component at frequencies 1 kHz and below (for results above 1 kHz, see the end of this section). The real component stayed approximately constant with respect to frequency below 1 kHz; at each time point, the impedance value at 1 kHz agreed well with the DC resistance (**Table S1**).

In order to estimate the contributions of each individual gel layer in a tetrameric gel cell, we first measured the resistance across a stack containing a full cell (high-salinity gel,

cation-selective gel, low-salinity gel, anion-selective gel, high-salinity gel), then measured the total resistance across a stack containing a high-salinity gel, a cation-selective gel, and a low-salinity gel (**Table S1**). Subtracting this resistance from that of a full cell yielded the resistance associated with an anion-selective membrane alone in the appropriate ionic environment, while completely eliminating the resistance of the low-salinity gel. (The resistance of each high-salinity gel was determined by direct DC measurement to be negligible, less than 2% of the resistance of a cell.) We determined the cation-selective membrane resistance in this way as well, then subtracted both from a full cell to obtain the resistance of the low-salinity gel, approximately 0.103 Ω m^2 (**Table S2**). A direct DC measurement of the resistance of the low-salinity gel gave a value of 0.105 Ω m^2, which agrees very well with the subtractive estimate and supports this approach; both measurements confirm that the low-salinity gel is the dominant resistance of a tetrameric gel cell.

The measuring scheme used for these experiments is subject to non-steady-state conditions, particularly in schemes where a low-salinity gel is in direct contact with a high-salinity gel containing a voltage-measuring electrode. The values obtained in **Table S1** and the direct low-salinity gel measurement mentioned earlier are averages of values obtained by extrapolating exponential fits of time-courses of resistance data back to the time when the gels were put in contact; therefore, the quantities calculated based on this data and summarized in **Table S2** should be considered as estimates due to the uncertainty associated with extrapolating time-dependent effects[28].

At frequencies between 1 kHz and 1 MHz, the impedance spectra of the measured systems often had a nonzero imaginary component and the corresponding Nyquist plots appeared to show a small portion of a semicircle of the type indicative of R(RQ) circuits. However, the capacitance detected was too small to obtain fits yielding reliable values of the resistances and capacitances that comprise each membrane's impedance[29]. Since we have

mainly considered the artificial electric organ presented here as a DC power source, and as the eel's own high-frequency volleys occur at frequencies of around 400 Hz,[30] we consider the DC resistance and impedance values below 1 kHz to be the appropriate descriptors on the time scales relevant for this work.

Table S1. Resistances of various gel arrangements measured by DC and AC methods.

Gel arrangement	DC area-normalized resistance (Ω m^2) (mean ± s.e.m.)	AC area-normalized impedance @ 1 kHz (Ω m^2) (mean ± s.e.m)
Full cell High-sal. | Cation-sel. | Low-sal. | Anion-sel. | High-sal. (*N* = 4)	0.186 ± 0.024	0.174 ± 0.019
High-sal. | Cation-sel. | Low-sal. (*N* = 3)	0.153 ± 0.008	0.153 ± 0.005
High-sal. | Anion-sel. | Low-sal. (*N* = 3)	0.136 ± 0.016	0.133 ± 0.027

Table S2. Estimated resistances of the individual component gels of tetrameric gel cells.

Gel	Area-normalized resistance estimated from DC measurements (Ω m^2)	Area-normalized impedance estimated from AC measurements @ 1 kHz (Ω m^2)
Cation-selective gel	0.050	0.041
Anion-selective gel	0.033	0.021
Low-salinity gel	0.103	0.112
High-salinity gel	< 0.002	< 0.002
Full cell	0.186	0.174

Supplementary Information 7. Ion-selective membranes enable lower resistances than charge-selective membranes

Part of the reason that the internal resistance of tetrameric hydrogel cells is significantly higher than the internal resistance of *Electrophorus*' electrocytes (**Table 1**) can be attributed indirectly to the fact that the selective gels used in this work are broadly

selective for cations or anions rather than having ion-specific selectivity. This choice was made for practical reasons: it is straightforward to imbue a hydrogel with a high cation/anion permeability ratio by including high concentrations of charged monomers in a gel framework, causing Donnan exclusion of co-ions but not counterions (see **Supplementary Information 1**). A gel with a high selectivity between ions of the same polarity (for Na^+ over K^+, for example) is far more difficult to realize; on the other hand, this selectivity is possible in electrocyte membranes due to the presence of highly specialized monodisperse nanoscale channels. However, the ion-selectivity inherent to electrocyte membranes allows both the extracellular and intracellular compartments to contain solutions at the usual physiological ionic strength between 150 and 200 mM[18,31] while maintaining large opposing gradients of the two permeant species. The intracellular and extracellular compartments do not contribute meaningfully to the total resistance of the system, which is mostly provided by the membranes[20]. By contrast, imposing large alternating gradients of ions across broadly charge-selective membranes necessitates that one of the two reservoirs in each cell must have a low ionic strength (to illustrate this, **Fig. 1b** and **d** compare the ionic strengths of the compartments in electrocytes to those in gel cells). The low-salinity reservoir gel in the artificial electric organ had an ionic strength of 15 mM and provided most of the electrical resistance of each tetrameric gel cell (**Extended Data Fig. 5, Supplementary Information 6**).

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