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Data Article

Geometrical and electrophysiological data of the moving membrane method for the osmotic water permeability of a lipid bilayer

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ABSTRACT

Data of the osmotic water permeability of a lipid bilayer (diphytanoylphosphaticylcholin) in the presence of cholesterol (30 mole%) are shown under the simultaneous measurement of bilayer tension. Detailed methods and procedures for evaluating the water permeability using the moving membrane method (K. Yano, M. Iwamoto, T. Koshiji & S. Oiki: Visualizing the Osmotic Water Permeability of a Lipid Bilayer under Measured Bilayer Tension Using a Moving Membrane Method. Journal of Membrane Science, 627 (2021) 119231) are presented. The planar lipid bilayer is formed in a glass capillary, separating two aqueous compartments with different osmolarities, and osmotically-driven water flux is visualized as membrane movements along the capillary. The water permeability was evaluated under constant membrane area and tension after correcting for the unstirred layer effect. In these measurements, geometrical features, such as the edge of the planar lipid bilayer and the contact angle between bilayer and monolayer, were image-analyzed. The unstirred layer was evaluated electrophysiologically, in which gramicidin A channel was employed. In the presence of an os-

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motic gradient, the gramicidin channel generates the streaming potential, and the measured streaming potential data and the derived water-ion coupling ratio (water flux/ion flux) are shown. Detailed descriptions of the integrated method of the moving membrane allow researchers to reproduce the experiment and give opportunities to examine water permeability of various types of membranes, including those containing aquaporins. The present data of osmotic water permeability are compared with the previously published data, while they neglected the bilayer tension.

Specifications Table

Subject	Physiology, Biophysics; Physical Sciences, Surfaces and Interfaces
Specific subject area	Osmotic water permeability of lipid bilayer under a measured bilayer tension
Type of data	Table Image Fig.
How data were acquired	Electrophysiological methods Image analysis Physicochemical calculations
Data format	Raw Analyzed
Parameters for data collection	The moving velocity of a lipid bilayer formed in a glass capillary under an osmotic gradient is measured by inspecting bilayer images. The osmotic water permeability for a measured bilayer area and tension is evaluated after correcting the unstirred layer. The streaming potential generated in the presence of the gramicidin channel was evaluated electrophysiologically.
Description of data collection	A lipid bilayer of diphytanoylphosphatidylcholine and cholesterol (30 mole%) formed in a glass capillary is subjected to move upon application of an osmotic gradient, and the velocity of the membrane was measured under a microscope (moving membrane method). From the membrane geometry, the bilayer area and tension were evaluated using an integrated method of image analysis and electrophysiology. Also, the unstirred layer was evaluated by a method using the gramicidin channel as a probe, and the streaming potential generated by the gramicidin channel was measured. Accordingly, osmotic water permeability of lipid bilayer in a fixed bilayer area and tension was evaluated.
Data source location	Institution: University of Fukui City/Town/Region: Fukui Country: Japan
Data accessibility	With the article
Related research article	Keita Yano, Masayuki Iwamoto, Takaaki Koshiji, Shigetoshi Oiki, Visualizing the Osmotic Water Permeability of a Lipid Bilayer under Measured Bilayer Tension Using a Moving Membrane Method. Journal of Membrane Science 627 (2021) 119231, https://doi.org/10.1016/j.memsci.2021.119231

Value of the Data

- The osmotic water permeability (P_f) of the lipid bilayer is an essential parameter for evaluating water flux across the cell membrane, fundamental for various cellular activities. However, evaluation is complex owing to numerous factors affecting the measurements. The moving membrane (MM) method circumvents previous problems and establishes it as an accurate and simple method for evaluating the P_f.

- Researchers in biological and physicochemical studies on the water permeability through membranes would benefit by acquiring an accurate and easy evaluation method and data thereby. The MM method is promising for evaluating the P_f of lipid bilayers with variable lipid compositions and can be extended for evaluating the P_f of aquaporins embedded therein.
- The P_f data presented here is an unprecedented reference under a measured membrane tension. The streaming potential data are necessary for evaluating the unstirred layer, but it is also valid for inferring molecular mechanisms of ion permeation through channel molecules.

1. Data Description

1.1. Raw data and their calculation for the P_f values

In the moving membrane method, the velocity of the moving membrane, vel_m, is measured visually (Table 1, lower), from which P_f is evaluated as [1]

$$P_f = -\frac{A_{cap}}{v_w}\frac{vel_m}{A_{mem}\,\Delta c_s} \quad (1)$$

where A_{cap} is the capillary cross-sectional area (μm^2), v_w is the partial molar volume of water (cm^3/mol), vel_m is the membrane velocity (μm/s), A_{mem} is the membrane area (μm^2), and Δc_s is the osmotic gradient (mOsm/L) (Table 1). In the P_f evaluation, correction of unstirred layer (UL) is a prerequisite, which is evaluated as follows. Both compartments contain the same NaCl concentration, and the current ratio of the gramicidin channel at ±100 mV, I_{+100}/I_{-100}, was measured (Table 1). I_{+100}/I_{-100} represents a concentration difference of permeating Na^+ ions at the channel entrance on both sides. Given a linear relationship of concentration and current amplitude at the measured concentration range, the polarization ratio (Table 1) indicates the local concentration polarization of permeating Na^+ across the membrane. This polarization contributes to the osmotic gradient ($\Delta Osm_{electrolyte}$ = [electrolyte bulk concentration] × [polarization ratio]). Urea is added to only one side of the compartments; thus, the concentration polarization contributed by urea is half of the polarization ratio obtained by currents through the gramicidin channel (ΔOsm_{urea} = [urea concentration] × [polarization ratio]/2)[1]. Accordingly, the osmotic gradient is the sum of the local concentration of urea and polarized concentration of Na^+.

1.2. Streaming potential of the gramicidin A channel at different osmolarity

The V_{stream} was measured at different ΔOsm, and the slope value was obtained as -5.66 ± 0.60 mV/ΔOsm (n=17) for K^+ (Fig. 1). Ion permeates through the gramicidin channel via the single-file mode, and V_{stream} was related to the water-ion coupling ratio ($CR_{w\text{-}i}$; water flux/ion flux) [2–4] as follows:

$$\frac{V_{stream}}{\Delta\pi} = -\frac{v_w}{z\,F}CR_{w-i} \quad (1)$$

where v_w is the partial water volume (Table 1), z is the valence of the current carrier, and F is the Faraday constant. The $CR_{w\text{-}i}$ value, thus obtained, was 12.3, which is consistent with earlier reports on the gramicidin A channel [4,5].

The V_{stream} is used for correcting the current-voltage curve of the gramicidin channel [1].

1.3. P_f value of DPhPC with cholesterol

The P_f value of a diphytanoylphosphocholine (DPhPC) membrane with 30 mole% cholesterol was evaluated. The I_{+100}/I_{-100} value was measured at the osmotic gradients (Fig. 2B; Table 2).

Table 1
Raw data to calculate the P_f values of DPhPC membrane. (Upper) Data for the UL correction. (Lower) Raw data of the membrane movements. P_f is calculated from Eq. (1) such that J_v/A_{mem} is divided by v_w and ΔOsm multiplied by 10^6. These data are plotted in the reference [1] Fig. 3B.

Osmolarity of urea (mOsm/L)	I_{+100} / I_{-100}	Polarization ratio (I_{+100} / I_{-100} - 1)	UL corrected Osmotic gradient (mOsm/L)	Capillary radius (mm)	Capillary cross sectional area (mm^2)	Partial molar volume of water (v_w: cm^3/mol)
200	1.018	0.0185	194.465			
400	1.04	0.04005	391.99			
600	1,061	0.06105	581.685	0.55	0.9503	18
800	1.078	0.077913	768.835			
1000	1.105	0.10541	947.295			

†100 mM NaCl both sides.

Osmolarity of urea (mOsm/ L)	Experimental number	Membrane movement distance (μm)	Elapsed time (sec)	Membrane velocity (vel_m: μm/s)	Volume flux (J_v: μm^3/s)	Membrane diameter (μm)	Membrane area (A: μm^2)	J_v/ A (μm/s)
200	1	21.9	690	0.03181	30,229	498	194,683	0.1553
	2	33.63	690	0.04874	46,318	620	301,754	0.1535
	3	26.90	690	0.03899	37,052	575	259,541	0.1428
	4	21.95	690	0.03181	30,229	566	251,479	0.1202
	5	17.7	690	0.02565	24,375	490	188,479	0.1293
	6	26.55	690	0.03848	36,568	578	262,256	0.1394
	7	23.01	690	0.03335	31,693	524	215,542	0.147
	8	30. 8	690	0.04463	42,412	524	215,542	0.1968
mean		25.305	690	0.036683	34,859.5	546.9	23,6159.5	0.14804
S.D.		1.967	0	0.002848	2706.37	16.999	14,714.2	0.00868
400	1	30.09	690	0.04361	41,443	497	193,902	0.2137
	2	31.51	690	0.04566	43,391	472	174,885	0.2481
	3	42.13	690	0.06105	58,016	491	189,249	0.3066
	4	48.5	690	0.07029	66,797	539	228,059	0.2929
	5	31.15	690	0.04515	42,906	429	144,472	0.297
	6	43.54	690	0.0631	59,964	524	215,542	0.2782
	7	41.06	690	0.05951	56,552	502	197,823	0.2859
mean		38.283	690	0.055481	52,724.1	493.49	191,990.3	0.2746
S.D.		2.974	0	0.00431	4095.7	14.64	11,119.807	0.013346
600	1	14.51	163	0.08904	84,615	593	276,044	0.3065
	2	25.13	254	0.09895	94,032	519	211,448	0.4447
	3	29.03	526	0.05519	52,447	395	122,480	0.4282
	4	9.91	175	0.05664	53,825	475	177,116	0.3039
	5	20.18	292	0.0691	65,666	454	161801	0.4058
	6	49.21	655	0.07512	71,387	483	183,132	0.3898
mean		24.662	344.2	0.074007	70,328.7	486.5	188,670.2	0.37982
S.D.		6.204	89.9	0.007821	7432.2	29.6	23,169.2	0.02718
800	1	60.18	690	0.08722	82,885	485	184,652	0.4489
	2	35.4	690	0.0513	48,750	348	95,067	0.5128
	3	111.16	690	0.1611	153,093	614	295,942	0.5173
	4	49.21	690	0.07131	67,766	458	164,665	0.4115
	5	76.49	690	0.1109	105,388	569	254,152	0.4147
	6	82.13	690	0.119	113,086	525	216,366	0.5227
	7	52.04	690	0.07542	71,672	443	154,055	0.4652
	8	54.52	690	0.079	75,074	435	148,542	0.5054
mean		65.14	690	0.094406	89714.3	484.6	189,180.1	0.47481
S.D.		9.015	0	0.013067	12,417.1	31.6	24,211.0	0.01742

(*continued on next page*)

Table 1 (*continued*)

Osmolarity of urea (mOsm/ L)	Experimental number	Membrane movement distance (μm)	Elapsed time (sec)	Membrane velocity (vel_m: μm/s)	Volume flux (J_v: $\mu m^3/s$)	Membrane diameter (μm)	Membrane area (A: μm^2)	J_v/ A (μm/s)
1000	1	63.72	573	0.1112	105,673	502	197,823	0.5342
	2	59.12	690	0.08568	81,422	459	165,385	0.4923
	3	65.49	690	0.09491	90,193	446	156,149	0.5776
	4	87.08	690	0.1262	119,928	545	233,165	0.5143
	5	68.32	690	0.09902	94,099	438	150,598	0.6248
	6	71.15	690	0.1031	97,976	455	162,515	0.6029
	7	75.76	690	0.1098	104,343	504	199,403	0.5233
	8	105.85	690	0.1534	145,776	552	239,193	0.6094
mean		74.561	675.4	0.110414	104,926	487.6	188,028.9	0.55985
S.D.		5.760	15.6	0.007997	7599.3	16.9	13,140.9	0.01888

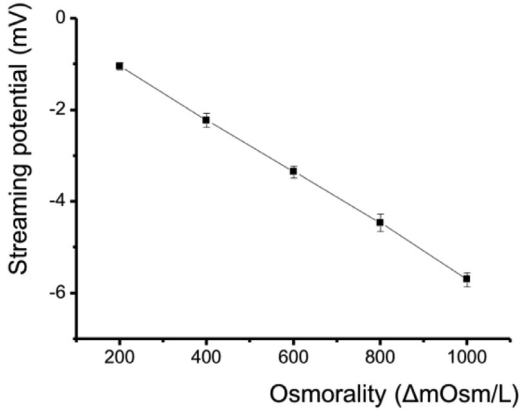

Fig. 1. The streaming potential as a function of osmotic gradients.

Measured J_v /*A* values were plotted as a function of the UL-uncorrected (black) and -corrected (red) osmotic gradient. The P_f value of 26.2 ± 0.31 μm/s was obtained through fitting the linear function to the UL-corrected data (Fig. 2A). In parallel, bilayer tension was evaluated as 1.44 ± 0.16 mN/m using a previously described method [6].

The previously published data, while they neglected the bilayer tension, are shown (Table 3).

2. Experimental Design, Materials and Methods

Preparation of Lipid Emulsions: DPhPC in chloroform (DphPC; 150 μL of 50 mg/mL: Avanti Polar Lipids, Alabaster, AL) was rotary evaporated to remove the solvent and was stored in a low-pressure environment of 17 hPa with a desiccator for six h or more [6,7]. It was then dissolved in 250 μL of hexadecane (50 mg/mL of hexadecane, Nacalai Tesque, Kyoto). For the cholesterol-containing emulsion, cholesterol (10 mg/mL) was mixed with 40 μg/mL DphPC solution in a 1:1 volume ratio.

Solutions: A 100-mM NaCl solution was used as a standard solution, and the osmolarity was measured using an osmometer (Osmometer 3250, Advanced Instruments, Inc., Norwood, MA) (165 mOsm/L). Different concentrations of urea (200, 400, 600, 800, and 100 mM) in 100 mM NaCl were prepared, and osmolarity was measured (362, 562, 758, 966, and 1164 mOsm/L, respectively).

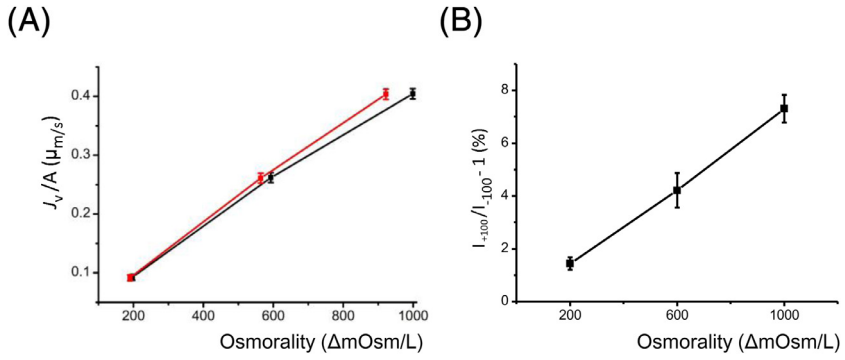

Fig. 2. P_f of a phosphatidylcholine membrane with 30 mole% cholesterol. A. J_v/A as a function of the osmotic gradient without (black) and with the UL correction (red). The P_f value was calculated as 26.20 ± 0.92 μm/s. B. The polarization ratio (I_{+100}/I_{-100} - 1) at different osmotic gradient.

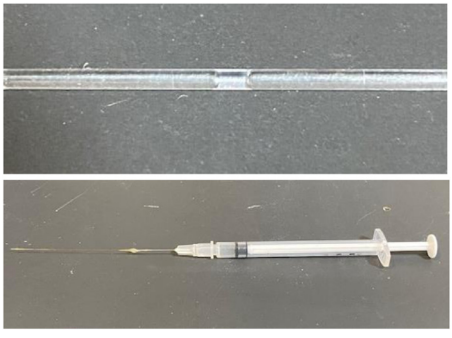

Fig. 3. The capillary and the syringe for aspirating the oil. The capillary was filled with electrolyte and oil successively. The bulky oil phase was aspirated with the syringe with polymicrocapillary glued at the tip of the needle.

Gramicidin A (Santa Cruz Biotechnology, Dallas, TX, USA) was dissolved in ethanol at 1 mmol/L ethanol solution as a stock solution [8]. It was further diluted in an aqueous solution.

Surface treatment of the capillary: A glass capillary (Borosilicate Glass Capillaries, TW150-4, World Precision Instruments, Inc., Sarasota, FL) with an inner diameter of 1.1 mm length of 50 mm was used. First, the capillary's inner surface was made hydrophobic to accommodate the interfacial monolayer. The surface was coated with SIGMACOTE (Sigma – Aldrich, St. Louis, MO) and stored for at least six h in a desiccator at 17 hPa. The hydrophobic surface was further coated with DphPC (40 mg/mL hexane) and then stored in a desiccator at 17 hPa for more than three h.

Glass capillary and syringe for drawing oil: Glass capillary filled with electrolytes and oil are shown (Fig. 3). The intercalated oil phase was aspirated using a syringe with a long fine tube of polymicrocapillary (200 μm in diameter, Polymicro Technologies, Inc., Phoenix, AX).

Electrode setting and electrophysiological measurements: Electrical measurements were performed for evaluating membrane capacitance and currents through the membrane-incorporated gramicidin A channel [9]. AgCl ink (BAS, 011464, Tokyo) was painted at one end for the capillary's inner surface [1]. For the other open end of the capillary, KCl-bridged Ag/AgCl electrodes were inserted into the electrolyte solution.

The membrane capacitance was measured by applying the ramp potential (±10 mV/ms). Given the specific membrane capacitance [1], the membrane area was estimated.

Image analysis for the membrane location and contact angle: The tangential view of the membrane (Fig. 4, left) was used to identify the membrane edge and evaluate the contact an-

Table 2
Raw data to calculate the P_f values of DPhPC with 30 mol% cholesterol. (Upper) Data for the UL correction. (Lower) Raw data of the membrane movements. P_f is calculated from Eq. (1) such that J_v/A_{mem} is divided by v_w and ΔOsm multiplied by 10^6. These data are plotted in Fig. 2.

Osmolarity of urea (mOsm/L)	I_{+100} / I_{-100}	Polarization ratio (I_{+100} / I_{-100} - 1)	UL corrected Osmotic gradient (mOsm/L)	Capillary radius (mm)	Capillary cross sectional area (mm^2)	Partial molar volume of water (v_w: cm^3/mol)
200	1.014	0.014	195.671			
600	1	0.042	587.364	0.55	0.9503	18
1000	1.073	0.073	963.48			

†100 mM NaCl both sides.

Osmolarity of urea (mOsm/ L)	Experi-mental number	Membrane movement distance (μm)	Elapsed time (sec)	Membrane velocity (vel_m: μm/s)	Volume flux (J_v: $μm^3$/s)	Membrane diameter (μm)	Membrane area (A: $μm^2$)	J_v/ A (μm/s)
200	1	5.65	374	0.01511	14,355	426.4	142,714	0.1006
	2	2.47	236	0.01047	9953	352.3	97,457	0.1021
	3	2.82	456	0.00619	5887	305.7	73,376	0.0802
	4	7.42	690	0.01075	10,212	375.7	110,776	0.0922
mean		4.590	439	0.01063	10,101	365.03	106,080	0.09378
S.D.		1.362	109.9	0.002101	1996.9	28.97	16,693	0.0058
600	1	13.08	351	0.03727	35,416	394.848	122,385	0.2894
	2	34.16	690	0.0495	47,042	456.543	163,619	0.2875
	3	1.82	70	0.02595	24,665	346.863	94,446	0.2612
	4	7.27	199	0.03652	34,704	415.413	135,466	0.2562
mean		14.080	327.5	0.037311	35,456.8	403.41675	128,979	0.27358
S.D.		8.171	154.4	0.00556	5283.6	26.327127	16,593.237	0.00999
1000	1	41.30	642	0.06433	61,135	436.435	149,523	0.4089
	2	53.69	690	0.07781	73,947	457	163,946	0.451
	3	40.55	690	0.05877	55,848	399.418	125,235	0.4459
	4	53.32	690	0.07727	73,430	461.113	166,911	0.4399
mean		47.215	678	0.069546	66,090	438.4915	151,403.75	0.43643
S.D.		4.197	13.9	0.005491	5218.12	16.279723	10,985.463	0.01091

gle. In earlier work, the shape of the torus around the bilayer was theoretically solved [10]. Here, the points at the monolayers contacting the bilayer and the contact angle were evaluated through functional fitting to the torus contour [6,11]. First, bilayer and monolayer outlines in the tangential image were extracted using image analysis software (ImageJ, U. S. National Institutes of Health, Bethesda, MD) (Fig. 4 right). Next, the outline of the monolayer region of either side of the bilayer was fitted to an ellipse (green curves) using data analysis software (Origin Pro; OriginLab, Northampton, MA, USA). Then, the bilayer diameter was determined from a distance between the intersection points of both ellipses. The slope of tangent lines at intersection points was calculated, which is the contact angle of each side, and they were averaged.

Bilayer tension measurements: The method for evaluating the bilayer tension was described in the previous paper [6]. The monolayer tension was evaluated by a conventional method using the Young-Lippmann principle [6,12,13],

$$\gamma_{mono} = C_{bi}\frac{{V_m}^2}{4\left(\cos\theta_0 - \cos\theta_{V_m}\right)} \tag{5}$$

where C_{bi} is the bilayer capacitance, V_m is the membrane potential, and θ_0 and θ_{Vm} are the contact angles at 0 mV and V_m mV, respectively. Step voltages (+50 to +200 mV with an increment of 50 mV) were applied successively; each time after relaxation, the contact angle between the

Table 3
P_f data from references. Historically accumulated P_f data, while the membrane tension is not evaluated.

P_f value (μm/s)	Lipid composition	Membrane	Method	Authors	Journal
19	egg PC	PLB	osmotic flow method	Hanai and Haydon	J. Theoret. Biol. (1966) 11, 370-382
44	PC	liposome	stopped flow	Reeves and Dowben	J. Membrane Biol. (1970) 3, 123-141
35-40	Egg PC, DOPC	liposome	osmotic method	Fettiplace	BBA (1978) 513, 1-10
37	GMO	PLB	Osmotic flow method	Dani and Levitt	Biophys. J. (1981) 35, 485-500
0.08∼0.3	DMPC,DPPC and other	liposome	stopped flow	Jansen and Blume	Biophys. J. (1995) 68, 997-1008
14.9±1.7	DphPC	liposome and PLB	chamber and light scattering	Hilmar, Zeidel	JBC (1996) 271 11627-11630
122∼662	PC (18:0, 18:1, 18:3, 22:6)	liposome	light scattering	Huster et al.	Biophys. J. (1997) 73, 855-864
35±5	egg PC	liposome	stopped flow	Dordas	J. Membrane Biol. (2000) 175, 95-105
34.4±3.5	PE+PS+PI+Chol	PLB	ion selective electrode	Krylov et al.	J. Gen. Physiol. (2001) 118, 333-339
21∼158	DLPE, DOPS, and other	liposome	stopped flow	Mathai et al.	J. Gen. Physiol. (2008) 131, 69-76
12	DphPC	PLB	DIB	Dixit et al.	Langmuir (2012) 28, 7442-7451
42±3	DphPC	PLB	DIB	Milianta et al.	Langmuir (2015) 31, 12187-12196
20-40	mouse erythrocyte	vesicle	microfluidics	Jin, Verkman	Lab Chip (2015) 15, 3380-3390

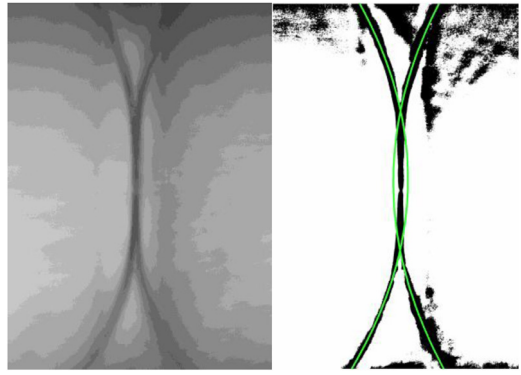

Fig. 4. The image of the bilayer and the torus and its contour with fitted lines (×400 magnification). For the bilayer area and the contact angle, the confluent points of the monolayers with the bilayer must be identified. Here, the contour of the image was fitted with an ellipse function (green lines).

monolayer in the membrane torus and the bilayer was measured (Fig. 4). Then, from the contact angle, the bilayer tension was evaluated using the Young principle:

$$\gamma_{bi} = 2\gamma_{mono}cos\theta \tag{6}$$

2.1. Streaming potential measurements for the gramicidin A channel

The use of the gA channel as a probe for the unstirred layer requires additional considerations. Under an osmotic gradient across the membrane, water flows through the gA channel. This flow generates the streaming potential by carrying cations through the pore under a single-file regime [14,15] even in the absence of an electrochemical potential gradient (Fig. 1).

Potassium activity (100 mM KCl) rather than concentration was set as identical in the solutions with and without the osmolyte using a potassium-selective electrode (model 9719, 720Aplus, Thermo Orion, Inc. Beverly, MA) [14]. The V_{stream} value was evaluated using the zero-current clamp mode (Fig. 1).

For the I-V curve measurements for the gramicidin channel, the streaming potential was corrected by adjusting the offset potential as zero mV under the current-clamp mode. By setting the offset potential, the net current through gA channels is nulled at 0 mV potential. The water flux through gA channels remains when the pore is empty of ions.

3. Experimental Setup

Photos of the experimental setup are shown (Fig. 5). A glass capillary set on the microscope stage is shown with the electrical connection (Fig. 5 left). The microscope is set on an anti-vibration Table 3. The electrophysiological setup, involving a patch-clamp amplifier, an analog-digital – digital-analog converter, and display for image analyses, is shown (Fig. 5 right).

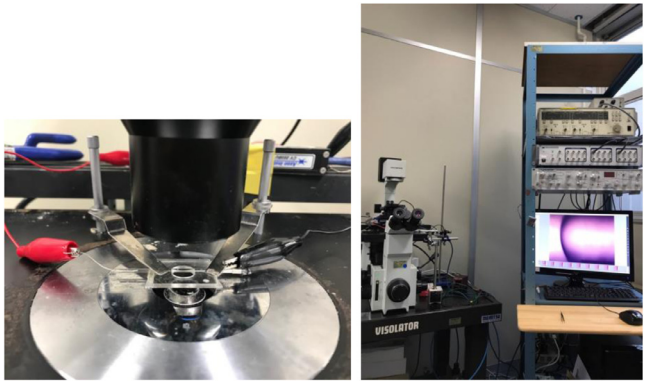

Fig. 5. The experimental setup. **Left**) The capillary set on the microscope stage, connected to the amplifier via the electrode. **Right**) the electrophysiological set with a camera for image analysis.

CRediT Author Statement

Keita Yano: Data curation, Writing- Original draft preparation. **Masayuki Iwamoto**: Conceptualization, Methodology, Image analysis. **Takaaki Koshiji:** Supervision. **Shigetoshi Oiki:** Conceptualization, Methodology, Writing- Reviewing and Editing.

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Ethical Statement

Not applicable.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships which have or could be perceived to have influenced the work reported in this article.

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