Figure 2 | Mechanism of electric-field sensing in perovskite nickelate. a, Comparison of *in situ* synchrotron XRR curves for pristine and water-treated SNO thin films after applying bias for 3 min and 9 min successively. The inset shows a magnified area of the XRR curves normalized to the oscillation peak for a scattering vector $Q \approx 0.16$ Å^{-1} (a.u., arbitrary units). **b**, Neutron reflectometry data, error bars and associated fits for pristine, hydrogenated and deuterated SNO thin films. Error bars represent one standard error. The inset shows a magnified area comparing oscillations normalized to the peak at $Q \approx 0.03$ Å^{-1}. **c**, X-ray absorption curves of the Ni L$_3$ edge of pristine and water-treated SNO, compared with that[25] of NiO. **d**, X-ray absorption curves of the O K edge of pristine and water-treated SNO. **e**, Optical transmission spectra of water-treated SNO, showing 100% increased transmissivity in the near-infrared. **f**, Comparison of the real (n) and imaginary (k) parts of the refractive indices of water-treated SNO and dry H$_2$-gas-treated SNO[27].

time of our SNO devices is in the same range as that of the elasmobranch electroreceptors (Extended Data Fig. 2f).

Charge transfer was observed during the water-mediated phase transition of SNO, as expected. A cathodic current peak (Extended Data Fig. 4a, b) appears in cyclic voltammograms of SNO at negative potentials, indicating the occurrence of a reduction reaction. The magnitude of the electric potential needed to trigger the reduction reaction of SNO increases with increasing pH value (Extended Data Fig. 4a), indicating the close relationship between water-mediated conductance modulation and the activity of protons in aqueous solutions. Fitting of the scan rate dependence of the cathodic current peak with the Randles–Sevcik equation[23] indicates that Ni^{3+} in SNO is almost fully reduced to Ni^{2+} after the reaction (Extended Data Fig. 4c and Supplementary Information section 4).

To investigate the microscopic mechanism of environmental sensing, *in situ* synchrotron X-ray reflectivity (XRR) measurements (Extended Data Fig. 5) were performed on SNO submerged in a 0.01 M KOH/water solution. Upon applying a bias potential of -1.5 V (Fig. 2a), the XRR results show a noticeable decrease in their oscillation period with increasing duration of the applied potential (Fig. 2a inset), indicating a substantial expansion of film thickness[24]. Synchrotron XRR investigations (Extended Data Fig. 6) show that such expansion occurs regardless of the solution type and is attributed to the increased lattice constant of SNO after the treatment.

Although it is extremely challenging to detect protons directly in solids, neutron scattering is among the best available techniques and is also sensitive to hydrogen isotopes. Neutron reflectivity curves for SNO are shown in Fig. 2b for the pristine film and films treated in D$_2$O (deuterated 'heavy' water) and H$_2$O solutions. The decrease in the oscillation period of the neutron reflectivity curves after H$_2$O or D$_2$O treatment (Fig. 2b inset) corresponds to a film expansion of about 6.9% and a decrease in film density (Supplementary Information section 5). The fitted neutron scattering length density profiles (Extended Data Fig. 7) show a considerable increase in the SNO region when H$_2$O is replaced with D$_2$O. This is consistent with the larger neutron scattering cross-section of D$^+$ relative to H$^+$. The isotopic substitution results therefore show clearly the intercalation and transport of H$^+$ (or D$^+$) from the solution to SNO, which is

similar to the ion transfer observed in the membranes of ampullae of Lorenzini.

Synchrotron X-ray absorption spectroscopy (XAS) measurements were carried out near the Ni L$_3$ edge and the O K edge of water-treated SNO. As Fig. 2c shows, with proton intercalation, the Ni L$_3$-edge absorption peak shifts its weight from 855 eV to 853 eV, similarly to the absorption edge seen[25] in NiO, indicating that Ni exhibits divalency after water treatment. Because the covalent nature of the Ni–O bond in SNO, where the electronic configuration of the ground state is dominated by the $3d^8\underline{L}$ state (where $\underline{L}$ denotes the existence of a ligand hole in the O $2p$ orbital)[25,26], we further studied the evolution of the O K edge after the water treatment. As Fig. 2d shows, suppression of the O K-edge absorption peak at 529 eV occurs after the treatment, indicating a reduced oxygen-projected density of unoccupied states caused by doping-induced band filling. Therefore, the XAS results of both the Ni L$_3$ edge and the O K edge demonstrate the formation of Ni^{2+} with the $3d^8$ configuration, resulting from charge transfer associated with proton intercalation after the water treatment. The charge transfer noted here is expected from the cyclic voltammetry observations.

Optical spectra of water-treated SNO were measured for further comparison with gas-phase proton-doped samples (that is, samples never exposed to water). As Fig. 2e shows, the transmissivity of water-treated SNO in the near- and mid-infrared frequency range increases compared to that of pristine SNO. As a result, SNO becomes more transparent in the infrared and visible wavelengths (Extended Data Fig. 8d). The reflectivity and absorptivity (Extended Data Fig. 8a, b) decrease concomitantly in water-treated SNO owing to the localization of charge carriers and opening of the optical bandgap. The real and imaginary parts (n and k, respectively) of the refractive index of water-treated SNO (Fig. 2f), which were calculated using transfer matrix formalism (Supplementary Information section 6), are in good agreement with those of HSNO treated with dry H$_2$ gas, without exposure to water[27]. This conclusion is further supported by finite-difference time-domain simulations of the optical spectra of water-treated SNO (Extended Data Fig. 8c). These results prove that the primary mechanism of sensing is proton intercalation into the SNO lattice, and not corrosion or degradation of the perovskite. The overall reaction taking place in SNO during electric potential sensing in an