Relationship of the Light-induced Proton Uptake in Bovine Retinal Outer Segment Fragments to Triton-induced Membrane Disruption and to Volume Changes*

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Light-induced proton uptake in bovine retinal outer segment (ROS) fragments was shown to be closely related to pH, salt concentration, membrane integrity, and perhaps secondarily to the volume of osmotic compartments. The principal findings were as follows:

1. As pH increased, both the discs and the plasmalemma swelled, and proton uptake markedly diminished.
2. As the discs were disrupted by increasing concentrations of Triton, proton uptake at slightly alkaline pH was supplanted by proton release.
3. Increasing the concentration of chloride salts caused increased H⁺ uptake roughly proportional to osmotic shrinkage of the ROS. Buffering by acetate prevented the measurement of proton uptake in the presence of acetate salts, although osmotic behavior of the ROS was similar to that observed in chloride salts. Although increasing the concentration of sucrose also resulted in osmotic shrinkage of the ROS, it was not accompanied by a systematic increase in the magnitude of proton uptake.
4. Light-induced H⁺ uptake was accompanied by small but reproducible changes in volume, probably of the discs. The magnitude and direction of these rapid volume changes were subject to influence by pH, solute, and other variables.

The precise mechanism by which the vertebrate photoreceptor converts a photon into a useful electrical signal is poorly understood. Recent attention has focused on the proposal that when rhodopsin is bleached, calcium ions may migrate from the rhodopsin-containing discs to the plasmalemma of the receptor outer segment, where they presumably block the dark conduction of sodium ions, resulting in hyperpolarization of the plasmalemma (1, 2). Although hyperpolarization is a measurable phenomenon, the experimental documentation of the alleged role of calcium thus far has been somewhat less than satisfying. Alternative possibilities, not necessarily exclusive of calcium movement, deserve exploration.

Morphological similarities among the ROS, mitochondria, chloroplasts, and other layered membranous organelles have long fascinated biologists. Major differences in lipid, protein, and chromophore composition, in the principal tasks required of these organelles, and in established pathways involved in the accomplishment of these tasks all argue against identical machinery in morphologically similar organelles. Yet certain broad analogies command interest. There is mounting evidence that organelles as disparate as chloroplasts, mitochondria, and photosynthetic or phototactic bacteria use layered membranes not only for the compartmentation of substrates needed for metabolic control, but for the separation of charged species as a way of storing energy intermediate to its ultimate conservation in the form of ATP (3-9).

The organized compartmentation and translocation of protons in particular has been identified as an important component of energy conservation in these systems. The possibility that a light-induced proton uptake, which we earlier described in the ROS (10), is also implicated in energy transduction appears to merit experimental investigation. In the earlier report, we observed that changes in sucrose concentration bore no systematic relationship to the light-induced proton uptake in the ROS and we prematurely concluded therefrom that the proton uptake was insensitive to changes in osmotic compartmentation within the ROS. Systematic examination of the relationship among osmotic variables, membrane volume and morphology, and the light-induced proton movement now indicates that the proton uptake is intimately related to osmotic compartmentation. Possible explanations for the apparent insensitivity of the phenomenon to sucrose concentration emerge.

METHODS

Bovine ROS fragments were separated from mitochondria and other contaminating particles on a linear sucrose density gradient, as...
Fig. 1 (legend on p. 1900).
Results of pH

The effects of varying the initial pH of the medium from acid to alkaline values are depicted in Fig. 1. In Fig. 1a, tracings of the light-induced pH increase are reproduced, for initial pH values of 5 and 8 in the presence of 0.12 M NaCl. Increasing initial pH, as earlier reported (10), markedly depressed the extent of the light-induced proton uptake. Fig. 1b reveals a close correspondence between the decrease in proton uptake and a decrease observed in light scattering by the ROS. The electron micrographs exhibit pronounced morphological changes between pH 5 and pH 7. As proton uptake and light-scattering decreased, the ROS discs opened up into distended, although still largely flattened, saccules. It is to be noted that this distention took place in the presence of isotonic salt concentration. It also appears that the space between adjacent discs is markedly enlarged in e, as though the plasmalemma itself had swollen. Further support for this inference is found in f, where wide spacing between adjacent discs can be seen, in contrast to that between the predominantly unswollen discs in d. In both cases, the plasmalemma has disappeared, possibly during the late stages of embedding of the material for sectioning.

Effects of Triton

Because of a previous observation (10) that a membrane-solubilizing concentration of Triton X-100 brought about a light-induced loss of protons from the ROS to the medium at pH higher than 6.2, it was endeavored in the present experiments to select concentrations of Triton just sufficient to bring about a reversal from net uptake to net loss of protons from the ROS at initial pH 7.3 and to relate these concentrations to the condition of the ROS membranes. Fig. 2 presents the outcome of these experiments at 0.12 mM salt concentration. In the presence of 0.022% Triton (a, top), the onset of the proton uptake was delayed several seconds after illumination began, and after 2½ min, net proton release occurred. At 0.078% Triton, protons were released (bottom) into the medium after a brief, small uptake. For concentrations of Triton intermediate between these two, pH tracings fell in an orderly way into the interval between the two tracings in a.

Light-scattering data for the entire range of Triton concentrations examined in this experiment are presented in Fig. 2b. At the lowest concentration (0.022%) the two data points reflect differences in light scattering measured twice under circumstances as similar as possible. Such differences were common at very low concentrations. In another experiment using a different ROS preparation, light scattering increased regularly as Triton concentration increased from 0.022% to 0.055% and then fell off sharply at 0.066%. In all cases, proton uptake co-varied with light scattering. Both measures depended primarily upon the degree of solubilization of the ROS membranes by detergent, a property related to the condition of the ROS, the length of time in suspension at 25°C, and the ratio of Triton to protein. In those instances when increased Triton concentration resulted in increased light-scattering and proton uptake, the ROS may have undergone an osmotically induced shrinkage, over and above that attributable to the presence of 0.12 M salt. Thus, at low concentrations Triton may behave like a nonpermeant solute, in spite of its destructive effect on the plasmalemma; for the most part they are closed, although ballooning (arrow) is evident. The disc fragments in d (× 20,261) are no longer confined by the plasmalemma, although a ribbon of plasmalemma can still be identified in association with the lower edges of the upper stack of fragments. Again, the discs are mostly closed, although two large vesicles at the left and numerous smaller vesicles elsewhere are probably derived from discs. In e (× 25,088) uniform swelling of the discs is evident, inside a largely intact plasmalemma. At the left can be seen isolated disc fragments which are also swollen. In f (× 21,584) are swollen disc fragments separated from the plasmalemma but still arrayed in parallel. Wide spaces between discs in e and f appear to indicate that the interdiscal space has also undergone swelling.
Effects of Triton on proton uptake, light-scattering, and morphology at pH 7.3 and 0.12 M NaCl. a, lower concentrations of Triton resulted in small, slow initial H+ uptake followed by a slower release of protons back to the medium; higher concentrations caused an earlier release of protons. b, light scattering, measured after proton uptake, underwent a decrease as Triton concentration increased, corresponding to disruption and solubilization of disc membranes, as seen in comparing c (x 20,548) with d (x 20,988). Although membrane deterioration was already underway at 0.033% Triton (c), parallel layers of discs were still in evidence, many still partly closed. At 0.055% Triton (d), organized disc fragments could no longer be found. The micrographs are not directly comparable to those in Fig. 1, because in the Triton experiments glutaraldehyde fixation of the ROS in suspension preceded sedimentation and postfixing with OsO4.

For the large light-scattering reduction which occurred between 0.033% and 0.055% Triton (Fig. 2b), the corresponding electron micrographs (Fig. 2, c and d) exhibited marked deterioration of the ROS membranes attributable to increasing Triton concentration. The reversal of the direction of proton movement found in the pH tracings appeared to be associated with a loss of organized disc structure, because the plasmalemma was already gone at 0.033%.

Osmotic Effects

Correlation between Light Scattering and Packed Pellet Volume—Increasing salt concentration of the medium earlier...
was shown in our laboratory to cause an approximately linear increase in light scattering as the ROS fragments underwent osmotic shrinkage (14). A linear relationship between packed pellet volume and decreasing osmolarity of salts also has been reported by Heller et al. for frog ROS (15). Direct comparison of light scattering and packed pellet volume as KCl concentration changes is made in Fig. 3. Selection of a sufficiently wide range of concentrations and enough data points permits an observation missed in earlier work, a decided break of the data into two straight lines. This break, first called to our attention in packed ROS pellet volume data by Darrell Fleischman, represents a serious departure from the Boyle-Van’t Hoff expectation for the ideal osmometer. However, the two measures of fragment volume coincide quite well at high concentrations, at the breakpoint, and until relatively low concentrations are reached (upper right). In that range, the correspondence breaks down because of variability in pellet volumes. This is to be expected from the fact that volume measurement (described in legend to Fig. 3) entails sedimentation and several subsequent steps, including at least 48 hours of vacuum drying and three separate weighing operations, whereas light scattering is direct and immediate.

Correlation between Light Scattering and Proton Uptake—When proton uptake and light-scattering were measured simultaneously, the regression of light-scattering data on proton uptake data appeared as in Fig. 4, a and b. In the case of KCl (a) an approximately linear regression line could be fitted to the data, implying that the shrinkage of these particular ROS fragments was linearly related to increasing proton uptake. A roughly linear relationship also obtained in the case of NaCl increase (b), further confirming earlier observations that the response of the ROS fragments, as prepared in our laboratory, is essentially the same to both Na+ and K+ cations.

The data in Table I, expanding on earlier work, indicate that even when chloride is replaced by the permeant acetate ion, impermeability to Na+ and K+ causes the ROS fragments to remain shrunken compared to their condition in NH4OAc, where both cation and anion are permeant. At approximately equimolar concentration, sucrose causes markedly less light scattering than the salts, which is consistent with the fact that its osmolarity is theoretically only half that of the electrolytes. On the other hand, CaCl2 should in theory elicit 1 1/2 times the osmotic response of the monovalent salts. Instead, its effect is about equal. Before concluding that the ROS fragments are leaky to CaCl2, however, direct osmometric or flame photometric determinations should be made, because CaCl2 is quite hygroscopic, and its effective concentration in solution may therefore be different from that calculated on the basis of its formula weight. Published osmotic coefficients are of little assistance with this problem, because they are determined for the hydrated form CaCl2·2H2O (16).

In the presence of acetate salts, proton uptake is virtually impossible to measure with the pH meter because of the greatly enlarged buffer capacity of the acetate ion compared to...
chloride. Therefore, the correlation between light-scattering and proton uptake could not be established in these media.

Sucrose Concentration and Proton Uptake

In sucrose alone (no salts or buffer), pH records are extremely noisy, making reliable measurement of the proton uptake all but impossible. Histidyl histidine and glycyglycine buffers at pH 5.0 and concentrations of 0.5 to 1.0 mM did not reduce noise appreciably. KOAc did, but also drastically reduced proton uptake, so that no appreciable advantage accrued from the use of these buffers. In the previous report (10) 5 mM MgCl₂ sufficiently quieted the electrode response so that proton uptake could be measured. It was found that the proton uptake was largely unrelated to sucrose concentration. The essentials of this finding were reconfirmed in the present study by measuring proton uptake in the presence of 5 mM NaCl, together with sucrose concentrations between 6.25 and 131.25 mM. Although pH records were noisy, it was determined that values of H⁺/rhodopsin ranged from 0.70 to 2.33 and were randomly correlated with sucrose concentration. The great variability of proton uptake in sucrose prevented the fitting of a plausible regression line relating this measure to light scattering. However, additional data relative to the correlation between the two measures are offered below.

Rapid Photo-induced Volume Changes

The data of Fig. 1 imply that any pH change should be accompanied by a corresponding change in volume of the ROS, as measured by light scattering. This inference should extend to the very small, rapid pH change caused by light. If measurements are made with sufficient care, it is possible to demonstrate rapid photo-induced changes in light scattering, above a high noise level resulting from stirring. The magnitude of such changes relative to osmotic changes induced by altering solute concentrations can be visualized in Fig. 5, a through d. Except for those in Fig. 5b, all of these changes are small enough to fall well within experimental error and thus to be overlooked unless deliberately sought. The changes in Fig. 5b are in the same direction as absorbance changes to be expected at lower wavelengths from the bleaching of rhodopsin and would very likely be interpreted as such without explicit precautions to eliminate such a possibility. Those precautions were taken in the present studies.

The recording traced in Fig. 6b demonstrates a light-induced reduction in light scattering from 1.29 to 1.28, measured simultaneously with the proton uptake in Fig. 6a. These two records correspond to the data point plotted at abscissa = 1.67, ordinate = 1.29 in Fig. 4a. Fig. 6c shows a similar light scattering decrease in 120 mM NaCl (see Fig. 4b). Similar decreases also were measured at pH 5.0 in 120 mM concentrations of KOAc, NaOAc, NH₄OAc (in spite of already marked swelling due to the permeability of the ROS membranes to this salt), and CaCl₂. In 5 mM NaCl (Fig. 6d) the change was smaller and biphasic, whereas in the absence of salt (Fig. 6e) and in sucrose (Fig. 6f), light caused a marked increase in light scattering. In both water (Fig. 6e) and sucrose (Fig. 6f) recording of pH change was extremely difficult because of the noise level, but a net proton uptake occurred.

The relatively large photo-induced light scattering increase in sucrose, like the photo-induced proton uptake in salt media (10), could be broken up into a step function by intermittent illumination. It exhibited marked inhibition by 10⁻⁴ M valinomycin (Calbiochem), a concentration which induces swelling in the ROS fragments when isotonic potassium acetate is the solute (14). Here, it produced the opposite effect, a scattering decrease, preventing the full light-induced increase from occurring. Gramicidin B (Calbiochem) at 10⁻⁴ M partially inhibited the photo-induced light scattering increase and also slowed it down.

The direction of the light scattering change was reversed by
Previously reliance on light scattering as a measure of ROS volume (14) is further validated by the present studies, and, in fact, the measure appears more reliable than packed pellet volume at low solute concentrations (Fig. 3). The combined electron micrographic and light-scattering data leave little doubt that light-scattering changes, as measured in this study, reflect volume changes in one or more ROS compartments. Even the smaller, light-induced changes observed in light-scattering would appear to be due to changes in disc volume. Although often proposed (vide infra) a light-induced change in macromolecular conformation of the ROS membrane has not yet been detected by the much more sophisticated means of circular dichroism (17, 18), and volume changes represent a more parsimonious interpretation of the data at this time.

The present studies reveal unequivocally that light-induced proton uptake in the ROS is closely related to pH, salt concentration, membrane integrity, and perhaps secondarily to the volume of osmotic compartments. The principal findings of the present studies are as follows:

1. As pH increased, both the discs and the plasmalemma swelled, and proton uptake markedly diminished (Fig. 1).
2. As the discs were disrupted by increasing concentrations of Triton, proton uptake at slightly alkaline pH was supplanted by proton release (Fig. 2).
3. Increasing the concentration of chloride salts caused increased H⁺ uptake roughly proportional to osmotic shrinkage of the ROS (Fig. 4). Buffering by acetate prevented the measurement of proton uptake in the presence of acetate salts, although osmotic behavior of the ROS was similar to that observed in chloride salts (Table I). Although increasing the concentration of sucrose also resulted in osmotic shrinkage of the ROS, it was not accompanied by a systematic increase in the magnitude of proton uptake.
4. Light-induced H⁺ uptake was accompanied by small but reproducible changes in volume, probably of the discs (Figs. 6 and 7). The magnitude and direction of these rapid changes were subject to influence by several variables, including pH, kind and concentration of solute, and perhaps the presence of ion-specific antibiotics. The most pronounced of these light-induced volume changes was a shrinkage in sucrose. It is uncertain whether the shrinkage seen in some preparations without added Mg²⁺ or Ca²⁺ was the same as that seen invariably when these cations were present.

Interpretation of the linearity displayed by data in the double reciprocal plots of Fig. 5 is required. The simplest explanation is that at lower concentrations of solutes (upper right segment) swelling, or perhaps breakage, induces permeability of the membrane compartment(s) to solute species excluded at higher concentrations. An alternative interpretation is that ROS fragments contain two or more membrane compartments with different permeability characteristics. The
Fig. 7. Electron micrographs (× 77,000) of ROS fixed in 1% OsO4 at pH 5.0, 0.25 M sucrose, 0.05 M KOAc before (left) and after (right) bleaching. The light-scattering record in the center shows an increase from A280 = 1.05 to 1.13 caused by bleaching which began at the arrow. Each of the small horizontal divisions is 5 s. The light-scattering medium contained 0.25 M sucrose and 5 mM MgCl2. No effect of bleaching was seen in the absence of MgCl2. ROS were sedimented for 15 min at 20,000 rpm in the Beckman No. 40 rotor prior to fixation. In the unbleached ROS, large numbers of the discs were found to be open. In the bleached ROS, most were closed. In the absence of MgCl2, bleaching did not cause closing of the discs.

Identity of such compartments might be revealed by applications of electron microscopic techniques such as those used by Stoner and Sirak (19) to resolve mitochondrial inner and outer membrane responses to osmotic titration.

Rapid, small amplitude volume changes induced by light correlated reasonably well in time with the proton uptake (Fig. 6). Electron micrographs (Fig. 7) appeared to reveal closing of the discs by light. It appears reasonable that salt, Triton, pH, and light may all affect proton uptake primarily by altering ionizable groups within the membrane structures, which secondarily cause osmotic volume changes. In the case of Triton, membrane disruption may occur simultaneously with ionic changes. The lack of consistent correlation between light-induced proton uptake and sucrose concentration, even in lightly salted sucrose, may be related to the fact that under most conditions light caused a relatively large volume change at the same time that proton uptake was being measured. Measured proton uptake may have been affected unpredictably. Another possibility is that one compartment has a different response to sucrose than does the other. Evidence supporting this interpretation comes from observations that the plasmalemma is relatively permeable to sucrose, even in lightly salted sucrose, may be related to the fact that under most conditions light caused a relatively large volume change at the same time that proton uptake was being measured. Measured proton uptake may have been affected unpredictably. Another possibility is that one compartment has a different response to sucrose than does the other. Evidence supporting this interpretation comes from observations that the plasmalemma is relatively permeable to sucrose, compared to the discs (20). Both Heller's and our own laboratories previously have reported osmotic anomalies of the ROS in sucrose, which bear further investigation (14, 15).

A comparison of the essential results from experiments conducted in our laboratory with observations made in the laboratories of Cone (21, 22) and of Heller (15, 23) is in order. Our observations with bovine ROS and those of Heller et al. (15) with frog ROS are in agreement with respect to the relative impermeability of the ROS to Na+, K+, Mg++, Ca++, chloride and phosphate ions, and sucrose, and with respect to the relative permeability of ammonium and acetate ions. Our observations agree with those from Cone's laboratory in that there occur important departures from ideal osmotic behavior. These add emphasis to the point made by Korenbrot and Cone (21) that the permeability characteristics studies in the isolated ROS may not be the same as those of the intact ROS in the retina. We also agree with these investigators that permeability characteristics attributed by Heller's (15, 23) group to the discs are more likely to be associated with both the plasmalemma and the discs. Our own data suggest the possibility of two or more distinct osmotic compartments in typical isolated ROS preparations, a point reinforced by the differences in permeability of the plasmalemma and the discs to sucrose (20).

In spite of the differences in measured dark permeability, all three laboratories have found the effects of light on permeability by measuring volume changes. Korenbrot and Cone (21) found that light prevented Na+ and Cl- influx, in effect facilitating a shrinkage when hyperosmotic NaCl was applied to frog ROS in pH 7.4 buffer. In Heller's laboratory, illumination of frog ROS in 1 mm Tris-Cl, pH 7.5, produced shrinkage in the presence of KCl and NaCl, but the shrinkages were slow, being measured by packed pellet volumes. In our own experiments described above, a rapid, photo-induced volume change was observed at 25° in unbuffered suspensions of large numbers of bovine ROS, the direction and amplitude of the change depending upon pH and solute. The volume change was correlated in time with the photo-induced proton uptake by the ROS, and in high sucrose at pH 5.0 may have entailed the extrusion of K+ ion and possibly the movement of Na+ as well, at least in the absence of added Mg++ or Ca++. Thus, all three laboratories report the apparent osmotic effects...
of light. Numerous other laboratories have reported permeability changes measured by flame photometry, counting of radioactivity, x-ray diffraction, electron microscopy, and other techniques which, by themselves, have little chance of measuring on-line permeability changes in real time (24–27), let alone of interpreting them physiologically.

The observation that Ca$^{2+}$ promotes a rapid, light-induced shrinkage in sucrose, apparently of the discs, may be related to the possibility that Ca$^{2+}$ acts as a communicating species between disc and plasmalemma. However, Mg$^{2+}$ also exerts the observed effect; thus, Ca$^{2+}$ may not be unique. It appears from the present experiments that the proton must also be considered for a role in translating effects of a photon from disc to plasmalemma. We share with Emrich (28) the belief that proton movement in response to light arises from conformational changes at or near the site of rhodopsin. Local pH changes subsequently may cause changes in membrane permeability to H', K', Na', Ca$^{2+}$, Mg$^{2+}$, or Cl$, resulting in the electrical changes required for excitation. Although some ionic permeability changes probably occur in the discs, it is the plasmalemma to which local ionic changes ultimately must be conveyed. Permeability changes also can be expected to cause volume changes, the direction and magnitude of which depend upon the osmotic conditions which prevail. Small volume changes, measured by zero-degree light-scattering, occurred almost always in the present experiments. Such measurements may provide the key to real time monitoring of ion redistribution in the ROS, a problem thus far resistant to the use of ion-specific electrodes because of the difficulty of detecting very small concentration changes, under isotonie prevailing concentrations 2 to 3 orders of magnitude greater.

Finally, the measurement in the present study of a rapid, pH-dependent light-induced volume change hitherto unreported bears directly upon the question of the occurrence of a conformation change associated with the bleaching of rhodopsin. A volume change cannot occur before such a conformation change, if present theories of excitation are correct (1, 2, 29) and might, in fact, occur considerably later. But detection of a conformation change has so far proven remarkably elusive. Although numerous investigators (30–39) have observed photo-induced changes in the visible or peptide regions of the ORD-CD spectrum of rhodopsin, neither Shichi et al. (37) nor we ourselves (17, 18) could detect such changes in ROS fragments which had not been subjected to detergents. A reinvestigation of these measures is indicated. If detection of a gross volume change can be obscured by an inappropriate selection of media conditions such as pH or buffer, so might a conformation change.

The clear effects in the present study of salts, Triton, and pH on both photo-induced proton movement and morphological change provide additional evidence for the alteration by light of the ROS membrane conformation, linked to altered proton binding on functional groups. This interpretation is consistent with the observations by Ostroy (40) of the correlation between rapid photo-induced pH changes and spectral changes, which he attributes to pK changes in rhodopsin.

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