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Articles

Membrane Skeleton Protein 4.1 in Inner Segments of Retinal Cones

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Retinal cone photoreceptors are polarized cells with discrete functional compartments. Little is known of the membrane-skeleton components in cones responsible for the maintenance of cellular morphology and compartmentalization of integral membrane proteins. The authors describe a high density of the membrane-skeleton protein 4.1 in the myoid region of cones in retinas of developing and adult frogs, and adult lizards, turtles, and chicks. In the developing retina, a discrete locus of protein 4.1 is first detected by immunocytochemistry in the cone myoid after the completion of photoreceptor synaptogenesis. Protein 4.1 immunoreactivity expands to line the plasma membrane of the myoid after cones attain their adult proportions. Nonerythroid α-spectrin and protein 4.1 colocalize in the cone myoid, and both are in close proximity to long bundles of f-actin that traverse the myoid and extend from the cone outer segment to the external limiting membrane. By analogy to the erythrocyte, where protein 4.1 modulates the interaction of spectrin and actin to regulate cell shape, the authors propose that protein 4.1 interacts with nonerythroid α-spectrin and f-actin in cones and plays a role in the maintenance of cone inner segment morphology. Invest Ophthalmol Vis Sci 32:1–7, 1991

The role of the spectrin-based membrane skeleton in regulation of cell morphology and immobilization of integral membrane proteins is well established in erythrocytes and is currently being investigated in other eukaryotic cells.[1–4] In erythrocytes, tetramers of the flexible rod-shaped spectrin interact with short filaments of actin to form a meshwork that lines the plasma membrane. Protein 4.1 binds simultaneously with the spectrin–actin meshwork and membrane attachment sites that include membrane phospholipid and integral membrane proteins. Phosphorylation of protein 4.1 modulates the affinity of spectrin and actin.[5] Thus, protein 4.1 tethers the membrane-associated cytoskeleton to the plasma membrane, immobilizes and compartmentalizes integral membrane proteins, and plays a central role in the regulation of membrane skeleton properties. Loss and/or oxidative damage of protein 4.1 in erythrocytes results in membrane fragility and loss of cellular deformability.[6–9]

Less is known about the retinal cone membrane skeleton. It is well established that actin bundles extend from the calycal processes to the external limiting membrane of cone inner segments[10–13] and are involved in light-induced contraction of cones in certain nonmammalian vertebrate species.[14,15] Spectrin and ankyrin are associated with cone plasma membrane from the external limiting membrane to the synaptic terminal, and spectrin has been described in cone inner segments.[16,17]

Recently, we localized protein 4.1 in developing and adult amphibian retinas.[18,19] In the present study, we have found an accumulation of protein 4.1 in the myoid region of retinal cones of developing and adult frogs, and adult lizards, turtles, and chicks. Significantly, we have also localized nonerythroid α-spectrin and f-actin in the same region of the cones, suggesting that these membrane-skeleton proteins interact to mediate cone functions.

Materials and Methods

Animal Maintenance

This study adhered to the ARVO Resolution on the Use of Animals in Research.

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The following species were used in this study: frogs (*Rana pipiens;* Kons, Germantown, WI, and *Xenopus laevis;* Nasco, Fort Atkinson, WI), chicks (*Gallus gallus domesticus;* Heisdorf and Nelson, Woodinville, WA), turtles (*Pseudemys elegans;* Carolina, Gladstone, OR) and lizards (*Anolis carolinensis;* Carolina). All animals were maintained on a 12-hr light:12-hr dark cycle in the University of Washington vivarium. The *X. laevis* adults were matured hormonally, and embryos were obtained and cultured as described previously.[20]

Antibody Preparation

Three antisera against protein 4.1 were used in this analysis. First, FPO2a antiserum was prepared in rabbits against previously described fusion protein (in the vector pRIT2T) that encodes the amino terminus of the *X. laevis* oocyte protein 4.1 between amino acids 41 and 254.[18] Second, FPO2b antiserum was prepared in rabbits similarly against another oocyte protein 4.1 fusion protein in the vector pRIT2T. FPO2b encodes a region of *X. laevis* oocyte protein 4.1 between amino acids 369 and 540 near the carboxy terminus.[18] To generate the FPO2b/pRIT2T construct, the FPO2b/EcoR1 insert was blunted with Klenow fragment and subcloned in frame into the Sma1 site of pRIT2T. *Escherichia coli* N4830 were transformed with the construct, and the protein was expressed as described by Giebelhaus et al.[18] Third, antiserum against purified chicken erythrocyte protein 4.1 was produced in rabbits as described in Spencer et al.[19] and affinity purified from western blots as described in Giebelhaus et al.[18]

Immunocytochemistry

Immunofluorescent localization of protein 4.1 in 10-μm cryostat sections of light-adapted developing and adult retinas was done as described in Spencer et al.[19] Briefly, protein 4.1 was localized with FPO2a antiserum, FPO2b antiserum, or affinity-purified antibodies against chicken erythrocyte protein 4.1. Nonerythroid α-spectrin was localized with antiserum from rabbits immunized with mouse brain α-spectrin (generously provided by Dr. Dorothy Roof). Primary antibodies were followed by goat anti-rabbit immunoglobulin G-fluorescein isothiocyanate-conjugated (IgG-FITC) secondary antibodies. Control sections were treated with preimmune FPO2a, FPO2b, chick erythrocyte protein 4.1, or mouse brain α-spectrin antiserum and followed by goat anti-rabbit IgG-FITC secondary antibodies. Cryostat sections of turtle retinas were double-labeled for protein 4.1 and F-actin by exposure to FPO2a antiserum, followed by goat anti-rabbit IgG-FITC; they then were treated for 30 min in 1:10 rhodamine-phalloidin (Molecular Probes, Eugene, OR) in phosphate-buffered saline with 0.25% Triton-X 100. All retinas were viewed by epifluorescence microscopy and photographed with Kodak Ektachrome 400 (Rochester, NY). The photographic exposure times of sections treated with immune or the corresponding preimmune sera were equal.

Western Blot

Protein was extracted from isolated retinas, separated by sodium dodecylsulfate polyacrylamide gel electrophoresis, blotted to nitrocellulose, and probed with antisera as in Giebelhaus et al.[20] The antisera used were generated against chicken α-spectrin[20] or mouse brain α-spectrin.

Results

We used two antisera against *X. laevis* oocyte protein 4.1 fusion proteins of nonoverlapping sequences and a third antiserum against chicken erythrocyte protein 4.1 to examine the distribution of membrane skeleton protein 4.1 in retinal cones of several species.

Cone photoreceptors in amphibian, reptilian, and avian species can be distinguished from rods by the presence of an oil droplet in the ellipsoid region of the distal inner segment (Figs. 1A, 2A). Proximal to the ellipsoid and extending to the external limiting membrane (Figs. 1A, 2A) is the myoid region of the inner segment.

The myoid region of single (Figs. 1B–C) and double (data not shown) cone inner segments of *R. pipiens* retina label intensely with both FPO2a and FPO2b antisera. Transected cone myoids reveal an unlabeled core (data not shown), suggesting that the label is associated with the plasma membrane. Additionally, a dim, diffuse fluorescence outlines outer nuclear layer somata vitread to the external limiting membrane, inner nuclear layer somata, and the inner and outer plexiform layers. Preimmune FPO2a (Fig. 1D) and FPO2b (data not shown) antisera do not label *R. pipiens* retinas.

Cones dominate the chick retina (Fig. 2A). The cone inner segments are reactive with FPO2a (Fig. 2B) and FPO2b (data not shown) antisera and affinity-purified antibodies prepared against purified chick erythrocyte protein 4.1 (Fig. 2C). The inner retina does not labeled with FPO2a or FPO2b antisera or affinity-purified FPO2a antibodies. Chick erythrocyte protein 4.1 preimmune antibodies do not label chick retinas (Fig. 2D), nor do chick erythrocyte protein 4.1 antibodies label *R. pipiens* retina (data not shown).

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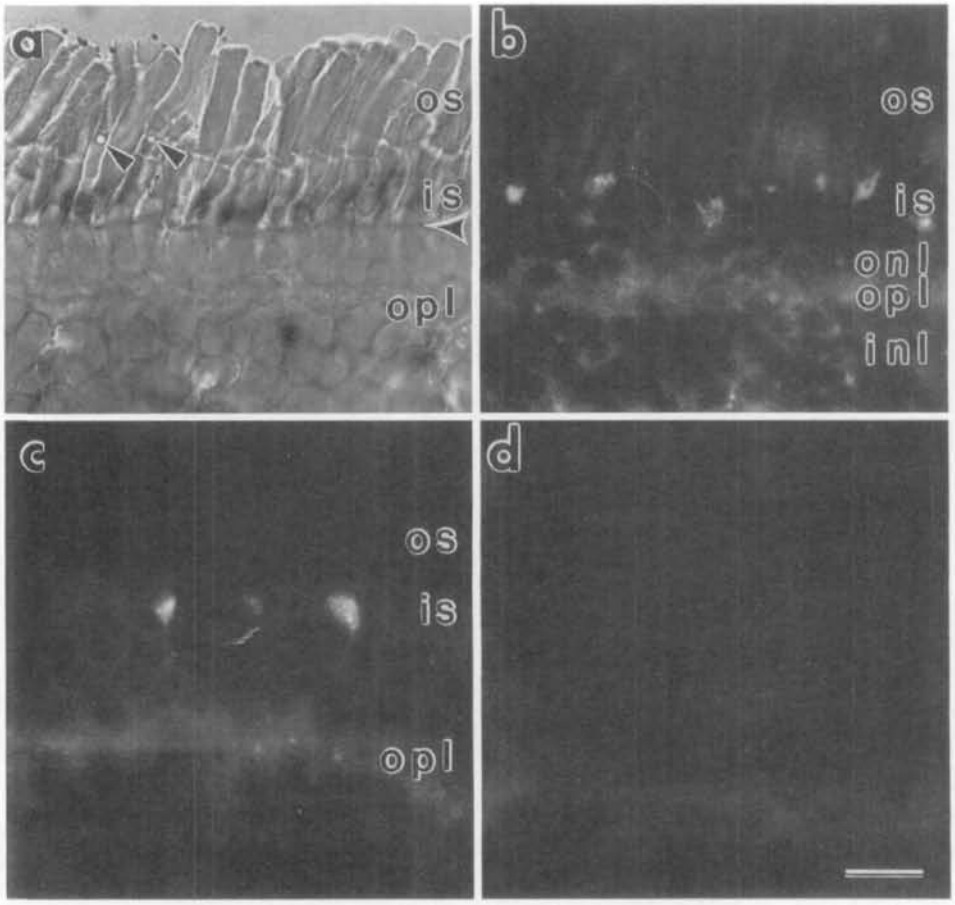

Fig. 1. Immunolabeling of protein 4.1 in *R. pipiens* retina. (**a**) Cones can be identified in retinal sections stained with Richardson's by an oil droplet in the ellipsoid region of the inner segment (small arrowhead). The myoid region of the inner segment is proximal to the ellipsoid and extends to the external limiting membrane (large arrowhead). is, inner segments; os, outer segment; opl, outer plexiform layer. (**b**) FPO2b antiserum labels the myoid region of cone inner segments (is). In addition, the outer (onl) and inner nuclear (inl) and outer plexiform (opl) layers label lightly. Photoreceptor outer segments (os) show dim autofluorescence. (**c**) FPO2a antiserum, like FPO2b antiserum, labels the myoid region of cone inner segments. The outer plexiform layer (opl) labels faintly. (**d**) FPO2a preimmune antiserum does not label *R. pipiens* retina. Photoreceptor outer segments show dim autofluorescence. Bar (a–d) = 20 μm.

These three independent antisera were used to confirm the localization of concentrated protein 4.1 in the myoid region of cones. We thought it was necessary to use several independent antisera since affinity purification of FPO2a antiserum using denatured FPO2a fusion protein selects for antibodies that intensely label cells of the inner retina of *R. pipiens* and *X. laevis*[19] but do not recognize the myoid region of cones. A possible explanation for the lack of labeling in the cone myoid with affinity-purified FPO2a antiserum is that antibodies that recognize cone myoid protein 4.1 do not bind to the denatured protein 4.1 fusion protein used for affinity purification. That two nonaffinity-purified antisera directed against distinct protein 4.1 fusion proteins label cone myoids in frog and chick retinas and that the myoid region of chick cones is also labeled with affinity-purified antibodies against chick erythrocyte protein 4.1 are compelling evidence that protein 4.1 is present in the myoid region of nonmammalian vertebrate cones.

Cone myoids in developing and adult *X. laevis* (Figs. 3A–D) and adult turtle (Fig. 4A) and lizard (data not shown) retinas are reactive with FPO2a antisera. In developing *X. laevis*, a small locus of protein 4.1 first appears vitread to the oil droplet in some cone myoids of day 8 (stage 49) tadpole retinas (Fig. 3A). By day 12 (stage 50), the locus of the label is apparent in most cone myoids, a diffuse fluorescence outlines most cone inner segments, and punctate label extends the length of cone outer segments (Fig. 3B). This locus of immunoreactivity expands until day 15 (stage 52, data not shown) and has a funnel-shaped distribution in the cone myoid of adult *X. laevis* retinas (Fig. 3C). With FPO2a antiserum, cones throughout adult *R. pipiens* (Figs. 1B–C), turtle (Fig. 4A), lizard, and chick (Figs. 2B–C) retinas are labeled; in adult *X. laevis*, labeled cones are found in the periphery of the retina, and unlabeled cones occur in the central retina (Fig. 3D). FPO2b antiserum also labels cones primarily in the periphery of adult *X. laevis* retinas (data not shown).

Turtle retinas, which are cone dominant, were double labeled with FPO2a antiserum and phalloidin. As in the other species examined, protein 4.1 is most prominent in the cone myoid and lines the plasma membrane (Fig. 4A). F-actin bundles, as identified by

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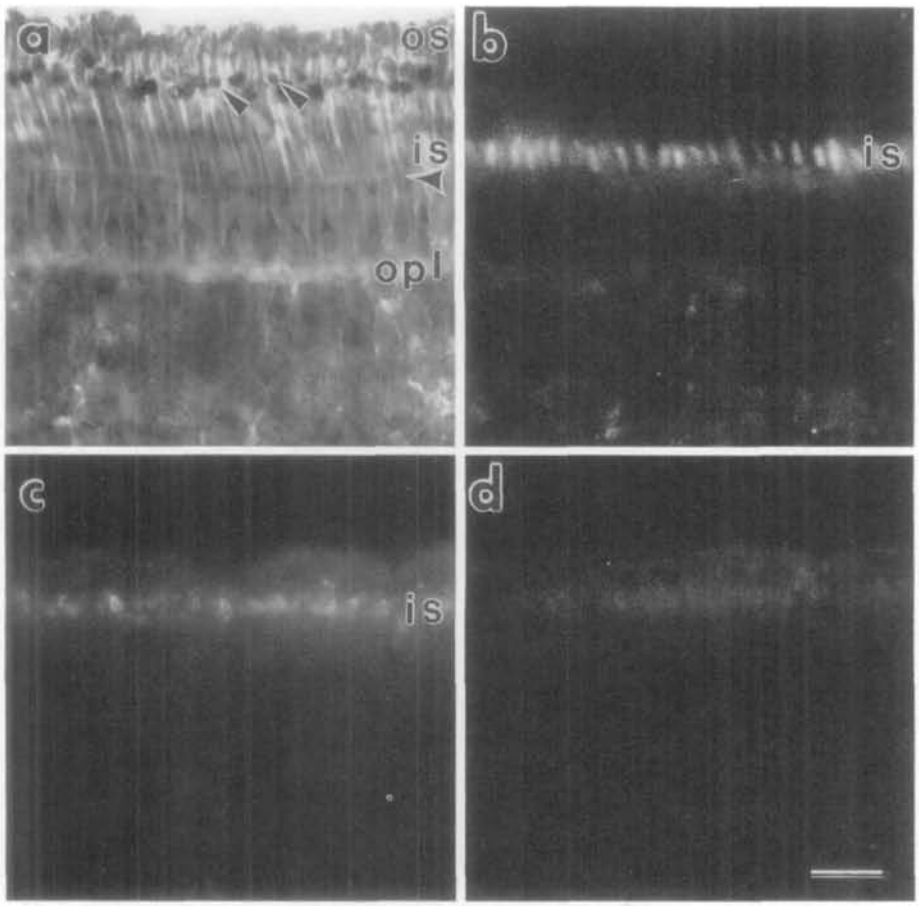

Fig. 2. Immunolabeling of protein 4.1 in chick retina. (**a**) Chick retinas are cone dominant as revealed by Richardson's stain. Small arrowheads point to oil droplets in the cone ellipsoid. os, outer segments; is, inner segments; large arrowhead, external limiting membrane, opl outer plexiform layer. (**b**) FPO2a antiserum labels cone inner segments (is). (**c**) Antibodies against chicken erythrocyte protein 4.1 also label cone inner segments (is). (**d**) Chicken erythrocyte protein 4.1 preimmune antibodies do not label chicken retina. Photoreceptors show dim autofluorescence. Bar (a–d) = 20 μm.

rhodamine-phallodin, traverse the cone myoids beneath the plasma membrane, including the region of densest protein 4.1, and extend from the outer segments to the external limiting membrane (Fig. 4B).

On sections of *R. pipiens* retina, nonerythroid α-spectrin colocalizes with protein 4.1 near the plasma membrane of cone myoids and has a punctate distribution (Fig. 5B). Nonerythroid α-spectrin preimmune antiserum does not label retinal sections from this species. A characterized antisera against nonerythroid α-spectrin from chickens[20] or the antiserum against mouse α-spectrin used for the described immunofluorescence analysis (Fig. 5B) both recognize a band of 240-kD in western-blot analysis of *R. pipiens* retinas (Fig. 5A, lanes 1,3).

Discussion

We recently localized protein 4.1 in developing and adult *X. laevis* and in adult *R. pipiens* retinas.[18,19] In this report we show that, in addition to the diffuse distribution of protein 4.1 in most retinal layers described in our previous studies, protein 4.1 is concentrated in the myoid region of cone inner segments of developing and adult *X. laevis*, adult *R. pipiens*, turtle, lizard, and chick retinas using three different antisera. Because FPO2a and FPO2b recognize domains near opposite termini of *X. laevis* oocyte protein 4.1 and both antisera label the myoid region of cones of two frog species, protein 4.1 in frog cones and *X. laevis* oocytes share common epitopes in these terminal domains. Similarly, the myoid region of chick cones are labeled with FPO2a and FPO2b antisera and chick erythrocyte protein 4.1 antibodies, providing evidence that protein 4.1 in chick cones and erythrocytes share common domains. Further analyses with antisera directed against protein 4.1 peptides will help elucidate the heterogeneity in protein 4.1 variants.

In our previous study, we demonstrated that during retinal development, protein 4.1 is first associated with the plasma membrane of photoreceptors after the final mitoses of all retinal neurons (day 5, stage 37).[19,21] Concomitant with the completion of retinal synaptogenesis (day 8, stage 49),[22,23] the distribution of protein 4.1 dramatically expands, and the protein is associated with the plasma membrane of photoreceptor outer and inner segments, the inner nuclear layer and ganglion cells, and the outer and inner plexiform layers.[19] At stage 49, the antibodies used in

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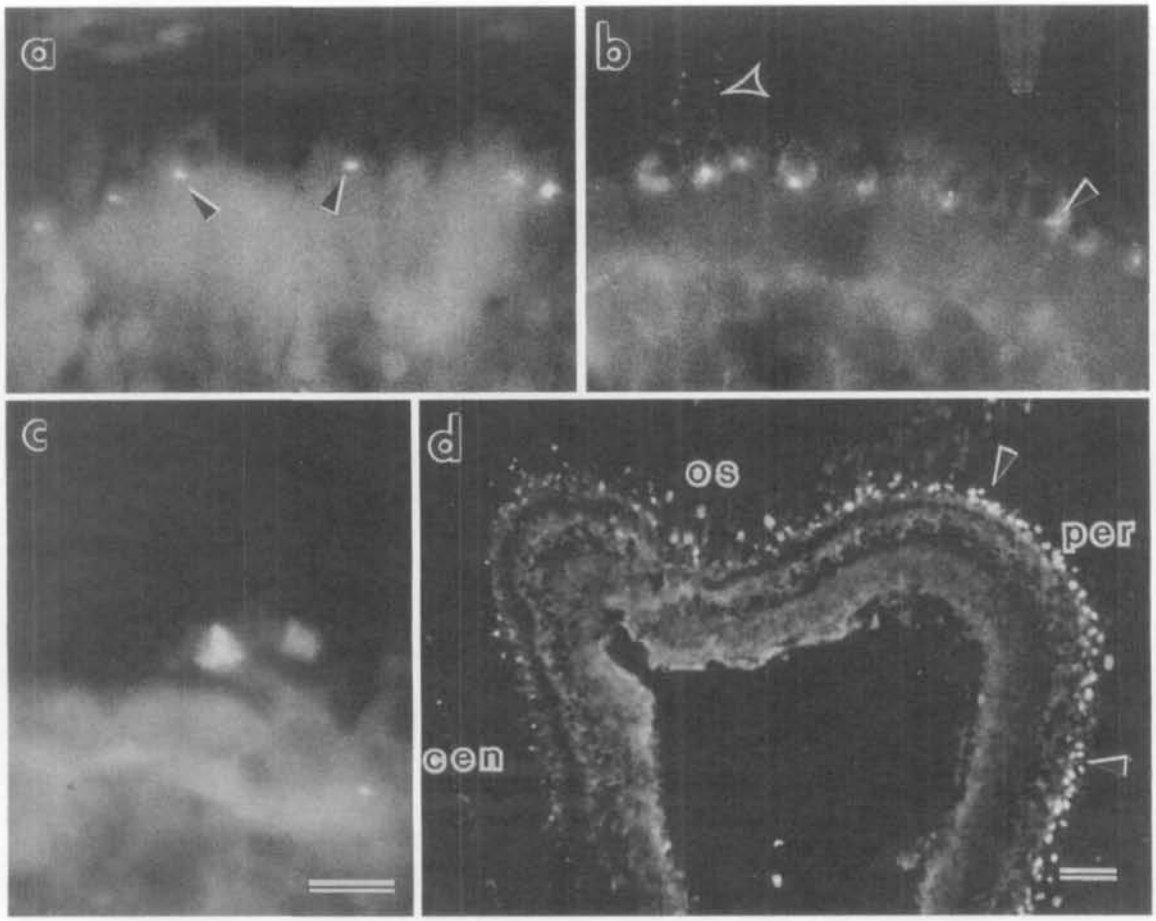

Fig. 3. Immunolabeling for protein 4.1 in developing and adult *X. laevis* retinas. (**a**) Eight-day (stage 49) retina. A bright locus of label is found vitread to the oil droplet in the inner segments of some developing photoreceptors (small arrowhead). (**b**) Twelve-day (stage 50). The locus of label persists in many photoreceptor inner segments (small arrowhead). Additionally, diffuse label is found in the myoid region and punctate label is found along the length of outer segments (large arrowhead) of some photoreceptors. (**c**) Adult retina. Two cones remain attached to the retina after detachment from the retinal pigment epithelium. Protein 4.1 label occurs in the myoid region of the inner segments. Bar (a–c) = 20 μm. (**d**) In adult *X. laevis*, photoreceptor inner segments (small arrowheads) in the periphery (per) of the retina label with FPO2a antiserum, while photoreceptor inner segments in the central retina (cen), including cones, rarely label. Note also label of outer and inner plexiform layers. os, outer segments. Bar (d) = 50 μm.

this study reveal a discrete, concentrated locus of protein 4.1 vitread to the cone oil droplet in the cone myoid. This locus of intense labeling expands with time. When all photoreceptors of *X. laevis* have reached their adult proportions (stage 53),[24] protein 4.1 immunoreactivity lines the plasma membrane in the cone myoid, imparting a funnel-shaped appearance that is also present in adult retinas. Punctate protein 4.1 label is also found in elongating cone outer segments (days 12–15, stage 50–52) but rarely in adult photoreceptor outer segments.

The role played by protein 4.1 in modulation of cell morphology through interaction with spectrin and actin is well established in erythrocytes. In this report we colocalize protein 4.1 and nonerythroid α-spectrin near the surface membrane of the myoid region of cone inner segments and demonstrate that these proteins are in proximity to a basket of f-actin filaments that extends from the inner segment calycal processes to the external limiting membrane. By analogy to erythrocytes (where protein 4.1 modulates the interaction of erythroid spectrin and actin filaments), we propose that protein 4.1 may modulate the interaction of nonerythroid α-spectrin and actin filaments in cone inner segments.

Specifically, protein 4.1 may play a role in cone retinomotor movements.[15] With light stimulation, the long slender stalk of the dark-adapted cone myoid contracts to form a broad, short connection between the ellipsoid and the external limiting membrane.[10] Burnside et al.[25] showed that this contraction occurs almost exclusively in the myoid region of the cone and is mediated by actin. Electron micrographs of detergent-lysed cones reveal that the plasma mem-

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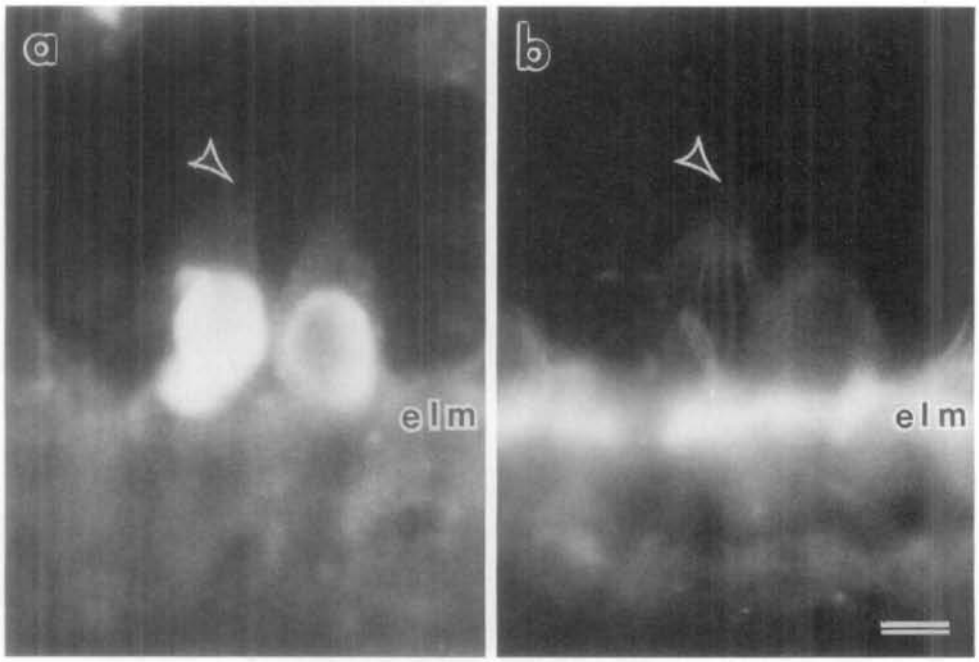

Fig. 4. Double labeling of protein 4.1 and f-actin in turtle cones. (**a**) FPO2a labels the myoid region of cones in turtle retina. This section bisects the cone on the right; the interior of the cone labels less intensely than the perimeter, indicating that protein 4.1 is associated with the plasma membrane of the myoid region. The large arrowhead points to the cone outer segment. (**b**) The same cones were labeled with rhodamine–phalloidin, revealing f-actin fibrils that extend from the external limiting membrane (elm) to the outer segment in the cone on the left. As discussed in (**a**), the cone on the right is bissected and f-actin bundles are absent in the interior of the cone. Therefore, f-actin is also associated with the plasma membrane in the myoid region. Bar (a, b) = 10 μm.

brane puckers in the myoid region during contraction and remains closely associated with actin bundles. Since protein 4.1 and nonerythroid α-spectrin are concentrated in the cone myoid, they may maintain cell morphology during contraction by providing membrane attachment sites for actin. We found protein 4.1 concentrated in the cone myoids of frogs, turtles, and chicks, three species reported to have retinomotor movements and well-developed actin filaments in the inner segment of cones.[11,14]

In addition to providing membrane attachment sites and modulating cell morphology, the simultaneous binding of protein 4.1 to integral membrane proteins and to the spectrin meshwork may function

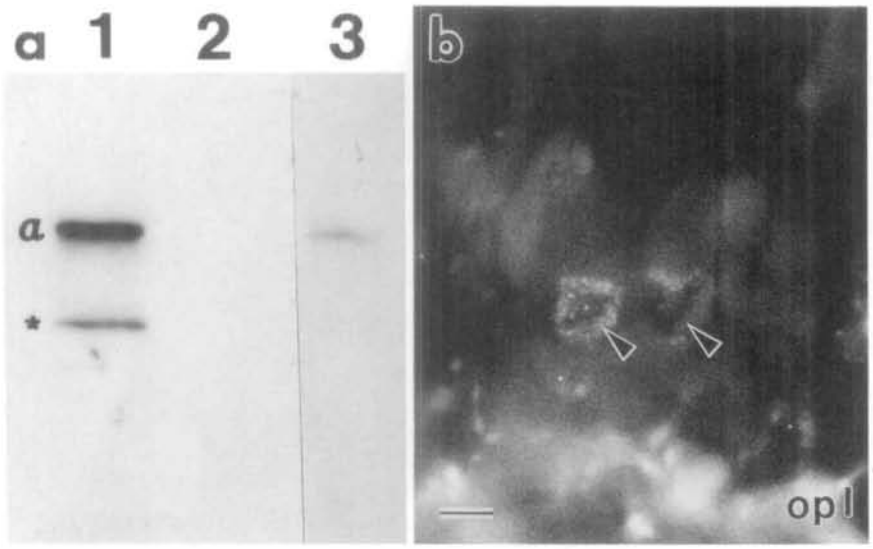

Fig. 5. Nonerythroid α-spectrin in *R. pipiens* retina. (**a**) Western blot analysis. Equivalent amounts of proteins isolated from adult *R. pipiens* retina were separated on SDS gels and blotted to nitrocellulose as described in *Methods*. The nitrocellulose strips were probed with antiserum to chicken α-spectrin[20] at 1:500 dilution (lane 1), preimmune serum against mouse α-spectrin (lane 2) or immune serum against mouse brain α-spectrin (lane 3) at 1:500 dilution. The (α) denotes the 240 kD band corresponding to nonerythroid α-spectrin. The (*) denotes a previously recognized breakdown product of nonerythroid α-spectrin.[28] (**b**) Punctate label is associated with the plasma membrane of the myoid region of cone inner segments (small arrowheads). Additionally, the outer plexiform layer (opl) labels heavily. Photoreceptor outer segments show dim autofluorescence. Bar = 10 μm.

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to inhibit the mobility and to restrict the distribution of integral membrane proteins. Cone photoreceptors are polarized cells and integral membrane proteins, such as Na^+/K^+ adenosine triphosphatase, have limited mobility and are restricted in distribution to the cone inner segment.[26,27] Although proteins are not yet identified that are restricted to the cone-myoid plasma membrane, it is conceivable that protein 4.1 could also function to tether integral membrane proteins in this region.

Key words: retina, cones, cytoskeleton, protein 4.1, spectrin

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