Arrangement of Human Erythrocyte Membrane Proteins*

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SUMMARY

The orientation of human erythrocyte membrane protein was examined by enzymic iodination using lactoperoxidase with the glucose-oxidase system for generating peroxide, followed by proteolytic digestion. The outer surface of intact cells was labeled with 125I and the cytoplasmic surface of either resealed ghosts containing lactoperoxidase or of inside-out vesicles was labeled with 131I. Following iodination, the outer surface (resealed ghosts) or the cytoplasmic surface (outer surface of inside-out vesicles) was digested with trypsin, chymotrypsin, or pronase. Sodium dodecyl sulfate gel electrophoresis of the isolated membranes revealed three major and several minor peaks of radioactivity. Their surface orientation, defined within the limits of the specificity of the probes used, was as follows: the three major peaks consist of: (a) a 90,000 to 100,000 molecular weight component labeled on both surfaces; its proteolytic digestion profile indicated that it spans the membrane in an asymmetric manner and that it is composed of more than one peptide; (b) the major red cell membrane glycoprotein (apparent molecular weight 60,000) which is labeled and digested at only the outer surface; and (c) peptide(s) of high molecular weight (~200,000), labeled and digested at only the cytoplasmic surface. The minor components include a glycoprotein of ~25,000 (apparent molecular weight) accessible to both surfaces and peptides of 60,000 to 70,000, 45,000, and 20,000, molecular weight labeled only on the inner surface.

Many of the functions of the erythrocyte membrane have been shown to be asymmetric; that is, certain activities or interactions with ligands are confined to the one surface or the other of the membrane. Among the best defined functional asymmetries is that of the (Na+,K+)-pump and associated ouabain-sensitive (Na+,K+)-ATPase (1). There is also a growing body of evidence that there is structural asymmetry with respect to the components of the erythrocyte membrane, i.e. protein (2-7).

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The abbreviations used are: (Na+,K+)-ATPase, Na+,K+-stimulated ATPase; PAS, periodic acid-Schiff; Na+-ATPase, Na+-stimulated ATPase.

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above for intact cells. The membrane protein concentration was 0.75 to 1.5 mg/ml.

**Vesicle Preparation**—Inside-out vesicles were prepared from iodinated red cells by the method of Steck et al. (24) with the modification of Perrone and Blostein (25) and washed and suspended in 20 mM Tris glycylglycine containing 0.1 mM MgCl₂. The “sidedness” and degree of sealing of these preparations were determined by measuring the percentage ouabain inhibition of the Na⁺-ATPase at 2 μM ATP relative to that of frozen and thawed ghosts (25).

**Treatment with Proteolytic Enzymes**—Proteolytic digestion of resealed ghosts (25% cell suspension) was done in 5 mM phosphate-buffered saline, pH 7.4: digestion of vesicles (0.3 to 0.5 mg of protein/ml) was carried out in 20 mM Tris glycylglycine containing 0.1 mM MgCl₂, pH 7.4. Treatment was for 10 min at 37°C at 0.1 mg/ml trypsin, chymotrypsin, or pronase, unless otherwise stated. The reaction was stopped with 0.2 to 0.4 mg/ml of soybean trypsin inhibitor or by addition of ice-cold buffer (5 volumes for vesicles, 15 volumes for ghosts). The preparations were then washed once with 50 to 100 volumes ice-cold buffer and then dissolved and prepared for electrophoresis (see below).

**Membrane Preparation and Electrophoresis**—Hemoglobin-free membranes of resealed ghosts were prepared by the method of Dodge et al. (26). Membranes were prepared for electrophoresis by dissolving them in 2% sodium dodecyl sulfate and heating for 3 min at 100°C followed by overnight dialysis against 2% sodium dodecyl sulfate containing 5 mM EDTA and 5 mM 2-mercaptoethanol. Prior to electrophoresis diithiothreitol was added (final concentration, 20 mM). Glycoprotein was extracted by the method of Hamaqué and Cleve (27). Extracted glycoproteins were dissolved in 2% sodium dodecyl sulfate containing 20 mM diithiothreitol and heated but not dialyzed. Electrophoresis was carried out by a modification of the method of Lenard (28) on 6, 7.5, or 10% gels, 8 cm long, using a 0.1 M sodium phosphate buffer, pH 7.0, containing 1% sodium dodecyl sulfate and run at 10 mA/gel until the tracking dye reached 6.5 cm. They were stained for protein with Coomassie blue and for carbohydrate with periodic acid-Schiff reagent by the method of Fairbanks et al. (29) with modifications of Cabantchik and Rothstein (30). Transferrin, bovine serum albumin, chymotrypsinogen, and cytochrome C were used as molecular weight markers for electrophoresis. For radioactivity profiles, the gels were divided into 2-mm minced segments and counted in a Packard gamma spectrometer. Other details are described elsewhere (3).

**RESULTS**

**131I Labeling of Outer Surface**

The lactoperoxidase-H₂O₂-catalyzed incorporation of iodide into intact erythrocytes could be markedly enhanced by preincubation of the cells in an isotonic medium for 1 to 2 hours. Furthermore, as the percentage of cells in the preincubation was decreased, the incorporation of 131I during the subsequent labeling (15 min at 1 μM KI) increased. As shown in Table I for example, the incorporation of label following a 2-hour preincubation of a 5% suspension was 31,357 atoms/cell and in other experiments varied between 25,000 and 50,000 atoms/cell, a value 5 to 10 times that of the unincubated cells, assuming 6.6 mg of protein/10⁶ cells (20). This phenomenon is similar to that of Morrison et al. in which it was shown that treatment of intact erythrocytes with a low concentration of trypsin resulted in the uncovering of "cryptic" sites (31). A typical radioactivity and protein profile of membrane prepared from 131I-labeled cells is shown in Fig. 1. The various protein components are designated according to Fairbanks et al. (29). Band III is the major 100,000 molecular weight protein component and PAS 1, the major glycoprotein also called glycophorin by Marchesi and co-workers (20). In the electrophoretic system used, there is incomplete separation of PAS 1 and PAS 2, the latter appearing as a trailing edge of the PAS 1 peak in both the radioactivity and PAS scans. Better separation of PAS 1 and 2 was achieved using 10% gels (see Fig. 4). Larger amounts of PAS 2 have been reported when the electrophoretic system is buffered with Tris (32, 33).

Results, prepared from 131I-labeled erythrocytes and relabeled on the outer surface, further incorporated 10,000 to 15,000 atoms/cell in a 15-min labeling period and occasionally there was appearance of radioactivity in a region designated as Band IV (see Ref. 34) in addition to the two major peaks, Band III and PAS I. There was, however, no difference in the pattern of radioactivity between preincubated and unincubated erythrocytes (not shown).

**131I Labeling of Inner Surface**

The radioactivity pattern of the 131I label on the cytoplasmic surface also was examined (see Fig. 4a, broken line) and, as described earlier (3-5), is characterized by two major peaks, one of large molecular weight corresponding to the spectrin protein(s) and a ~100,000 molecular weight polypeptide fraction at the same mobility as Band III labeled on the outer surface. As shown in Fig. 4a which depicts resealed ghosts labeled with 125I inside and 131I outside, there are minor components of molecular weights 20,000, 45,000, and 60,000 to 70,000, the last component sometimes appearing as two peaks. The externally labeled 131I peak for PAS 1 lies between the 45,000 and 60,000 molecular weight peaks. Labeling of the external surface (131I labeling of red cells) and the cytoplasmic surface (125I labeling of inside-out vesicles, c.f. Fig. 2) varied linearly with iodide concentration (0.01 to 1 μM iodide, not shown).

The failure to label the glycoprotein of resealed ghosts on the cytoplasmic surface did not appear to be due to unfavorable intracellular conditions such as peroxide-utilizing enzymes or competing soluble proteins, or both, as suggested by others (35, 36) since similar results were obtained if the cytoplasmic surface was labeled using inside-out vesicles (Fig. 2a). The peptides labeled from the cytoplasmic surface and appearing in the same region of the gel as PAS 1 can be distinguished from it by the following criteria.

1. Although these 131I-labeled components appear in the same general region of the gel as PAS 1, the exact mobilities of the radioactivity peaks are different from the mobility of the 131I-labeled PAS 1 peak, i.e., in the experiment shown (Fig. 2a) the 131I peak of PAS 1 lies between the 60,000 to 70,000 and 45,000 molecular weight 131I peaks; since both isotopes are on the same

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<th>Cell density during preincubation</th>
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<tr>
<td>-20%</td>
<td>3,205 8</td>
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<tr>
<td>5%</td>
<td>9,932 25</td>
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<tr>
<td>25%</td>
<td>21,806 55</td>
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<td>5%</td>
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membrane preparation, compared in the same gel, these are true differences in mobility.

2. Glycoproteins from these double-labeled inside-out vesicles, extracted by the method of Hamaguchi and Cleve (27), contained only small quantities of $^{131}I$ radioactivity, indicating that the peptides labeled from the cytoplasmic surface were not extracted with PAS 1. Whereas the total incorporation of iodide was 62.4 pmol/mg on the outer surface and 93.1 pmol/mg on the cytoplasmic surface, the labeling of extracted PAS 1 was 3.8 pmol on the outer surface and 0.07 pmol on the cytoplasmic surface in the peaks on the gel containing the glycoprotein extracted from 100 to 150 µg of membrane protein.

Because PAS 1 and PAS 2 could not be clearly distinguished on 7.5% gels, separation of glycoprotein of double-labeled vesicles was carried out using 10% gels (Fig. 3). As shown in Fig. 3b, the radioactivity ratio $^{125}I$ : $^{131}I$ in PAS 1 was 56 : 1. This represents 11.6 pmol (external surface) to 0.2 pmol (cytoplasmic surface) in a gel containing the glycoprotein extracted from 300 to 400 µg of membrane protein. It is possible, moreover, that this relatively small amount of labeling (0.07 pmol, Fig. 2c, and 0.20 pmol, Fig. 3b) is due to relabeling of broken or unsealed vesicles (c.f. labeling of 5 to 8% surface carbohydrate of inside-out vesicles using the galactose oxidase technique, Ref. 37). To monitor the degree of sealing of the inside-out vesicles, the sensitivity of Na$^+$-ATPase to ouabain-inhibition was measured (25) since the substrate (ATP) site for these vesicles is on the outer (cytoplasmic) surface, while the ouabain-binding site is on the inner surface (1, 25). It was observed that the degree of ouabain-inhibition varied from 0.7%, presumably the best, to 26%, the least well sealed preparations.

Trans-effects of Proteolytic Enzymes

To further delineate the disposition of the surface proteins, membranes, labeled on the outer surface with $^{125}I$ and cytoplasmic surface with $^{131}I$, were digested on either the outer surface using resealed ghosts or the cytoplasmic surface using inside-out vesicles. The proteolytic enzymes used for digestion were trypsin, chymotrypsin, and pronase.
FIG. 3. Glycoprotein of iodinated inside-out vesicles. Vesicles prepared from $^{125}$I-labeled red cells were reiodinated (cytoplasmic surface) with $^{131}$I. Glycoproteins were extracted (27) and subjected to electrophoresis on 10% gels. a, scan at 560 nm of gel stained with PAS; b, radioactivity profile. The ratio of $^{125}$I added (cpm) to $^{131}$I added (cpm) = 1.0.

Outer Surface—Treatment of resealed ghosts with trypsin had no effect on the labeling pattern of the cytoplasmic surface and on the outer surface, affected only the major glycoprotein, PAS 1, reducing its radioactivity peak, although not completely (Fig. 4c). The protein scan (Coomassie blue-stained pattern) was not altered by trypsin (Fig. 5c). There was no difference in the degree or pattern of labeling if resealed ghosts were first digested with trypsin on the outside and then iodinated inside or first iodinated and then digested (not shown). Thus, trypsin treatment on the outer, iodinated surface did not increase the accessibility of any proteins on the inner surface.

Pronase, at the outer surface (resealed ghosts), digested the 100,000 molecular weight trypsin-resistant component in addition to the major glycoprotein (Fig. 4b). A new Coomassie blue-positive peak (Fig. 5b) and a new radioactivity peak (Fig. 4b) corresponding to a molecular weight of 60,000 to 70,000 containing both $^{125}$I and $^{131}$I appeared, presumably a product of the 100,000 molecular weight polypeptide, as shown by other investigators (7, 18). The conclusion that the double-labeled 60,000 to 70,000 molecular component is a product of Band III is substantiated by the following results: when ghosts were treated first with trypsin to digest PAS 1 and then exposed to pronase the radioactivity pattern (Fig. 4d) was virtually identical to that obtained following digestion with pronase alone (Fig. 4b). The appearance of both isotopes in one peak after digestion on one surface indicates that the 100,000 molecular weight is polypeptide spanning the membrane rather than two classes of polypeptide, one on each surface of the membrane.

Inner Surface—As shown in Fig. 6, treatment of double-labeled inside-out vesicles with proteolytic enzymes showed that all the proteins accessible to lactoperoxidase are accessible to chymotrypsin (Fig. 6b), trypsin (Fig. 6c), and pronase (Fig. 6d). In all three cases the 100,000 molecular weight labeled protein was digested from the cytoplasmic surface and $^{25}$I radioactivity.
FIG. 6. Proteolytic digestion of $^{125}$I($^{131}$I)-labeled inside-out vesicles. Inside-out vesicles derived from $^{131}$I-labeled red cells (148 pmol/mg of protein) were relabeled on the cytoplasmic surface (outer surface of vesicles) with $^{131}$I (106 pmol/mg of protein) and then treated with proteolytic enzymes for 10 min at an enzyme concentration of 0.1 mg/ml. The vesicles were washed, dissolved, and subjected to sodium dodecyl sulfate polyacrylamide gel electrophoresis on 7.5% gels. a, control, no enzyme; b, chymotrypsin; c, trypsin; d, pronase. The ratio $^{125}$I added (cpm) to $^{131}$I added (cpm) = 0.5.

on the outer surface could be found in products of lower molecular weight in the same region as the major glycoprotein (60,000 molecular weight) or at 20,000 molecular weight, or both. A significant change in the mobility of the PAS 1 peak could not be detected (Fig. 7) whereas PAS 3 was digested by pronase. Although trypsin removed most of the double-labeled 100,000 molecular weight material, a radioactive, trypsin-resistant component of 110,000 molecular weight remained (Fig. 6c), corresponding to a Coomassie blue-positive peak (Fig. 8). The inability of trypsin to digest completely Band III in inside-out vesicles, as measured by protein staining, has also been shown previously by Steck and co-workers (2, 38).

A test of the effect of trypsin concentration on the digestion profile of inside-out vesicles was carried out in an effort to determine if the trypsin-resistant, 110,000 molecular weight component shown in Fig. 6c was due to incomplete digestion. As seen in Fig. 9 even at the lowest concentration of trypsin used (1 μg/ml), most of the double-labeled 100,000 molecular weight material was digested and appeared in the major glycoprotein region. Both $^{125}$I and $^{131}$I radioactivity appeared in this product. Further digestion with higher concentrations (up to 100 μg/ml) did not affect the remaining 110,000 molecular weight material but does further digest the products, completely removing the $^{131}$I radioactivity and yielding two smaller $^{125}$I products which run as shoulders to PAS 1 on these gels. This was more evident when electrophoresis was carried out on longer gels (not shown). It has not been determined if these two products are due to sequential digestion of one polypeptide or due to digestion of two different polypeptides. The trypsin-resistant peptide which contains only $^{125}$I radioactivity may, however, extend through the membrane because it is accessible to both chymotrypsin and pronase from the cytoplasmic surface (Fig. 6, b and d).

In an effort to determine if the digestion of surface protein could result in exposure of other proteins not previously accessible to iodination, notably PAS 1, inside-out vesicles were digested mildly with 1 (not shown) or 5 μg/ml of trypsin (Fig. 2b). They then were labeled with $^{131}$I. The resulting radioactivity profile was similar to that obtained by prior labeling and then digesting (c.f. Fig. 9c). Since the iodinatable products of the 100,000 molecular weight material appeared in the same region of the gels as PAS 1, (compare Fig. 2b with the control, Fig. 2a) the glycoproteins were extracted by the method of Hamaguchi and Cleve (27) and their radioactivity profile was examined. As shown in Fig. 2d there was virtually no $^{131}$I-labeling of PAS 1.

DISCUSSION

The conditions of mild iodination used in these experiments (1 μM iodide at high cell density and a peroxide-generating system) were selected in an effort to effect optimal labeling and, at the same time, to avoid anomalous results (39) and possible membrane damage due to excessive iodination and oxidation. Although it may be argued that this could lead to disparate labeling of groups of different reactivities (6), we have not been
The observation that generally similar profiles of labeling were obtained in the different preparations also support the conclusion that the methods used for membrane isolation led to only minor changes, if any, in accessibility of the proteins examined. Thus, although protein rearrangement is an inherent problem in this type of study (40), the radioactivity profiles of the outer surface of intact red cells and resealed ghosts are similar except for Band IV (see “Results” and Ref. 34); the profiles of the labeled cytoplasmic surface of resealed ghosts and inside-out vesicles are also similar, except for the apparent loss of some components from inside-out vesicles, mainly some of the spectrin and Band V (see also Ref. 29). In a recent study, Whiteley and Berg also have observed similar profiles using small molecular probes of the two surfaces of intact cells and ghosts (6).

In the present study the importance of evaluating the labeling of one membrane surface in terms of the sidedness or leakiness of the preparation used is emphasized. Thus we have shown that glycoporphin is inaccessible to iodination at the cytoplasmic surface when either of the following preparations is used: (a) resealed cells prepared under conditions which favor maximal resealing to cations (41), or (b) inside-out vesicles in which the sidedness or leakiness was assessed in terms of the sensitivity of Na+ ATPase to ouabain (26).

Our inability to show that the major glycoprotein, PAS 1, is accessible to enzymic iodination at the cytoplasmic surface of the red cell, is similar to results reported by Shin and Carraway using resealed ghosts (4). In contrast other workers have reported iodination of PAS 1 at the cytoplasmic surface (5, 35, 42) although it should be pointed out that their data do not indicate the labeling in terms of the moles iodide incorporated per mg of protein, or per cell, of the cytoplasmic surface relative to external surface (35, 42).

The present results raise doubt but do not show conclusively that PAS 1 is not exposed to the cytoplasmic surface of the red cell. Plausible explanations for the conflicting results are as follows.

1. Amino acid residues are exposed but are insensitive to the particular probe used. This possibility is supported by the results of Bretecher (11) showing labeling at the cytoplasmic surface using formylmethionyl sulphone methyl phosphate.

2. One or two tyrosine(s) on the COOH-terminal end of glycoporphin (45) are buried under other surface proteins, e.g. under spectrin, as suggested by Shin and Carraway (4) and consistent with the transmembrane association of spectrin and glycoporphin (44); this, in turn, may be indirect, e.g. via the major 100,000 molecular weight protein which spans the membrane and is found in the same particles as glycoporphin (45). Our inability to either detect digestion of PAS 1 or to render PAS 1 accessible to iodination after mild trypsin treatment of inside-out vesicles may not rule out completely this possibility. Some digestion of PAS 1 by proteolysis of the cytoplasmic surface was observed by Steck et al. (2, 38).

3. Differences in accessibility could be related to the differences in the preparations examined such as unsealed compared to sealed, ion-impermeable ghosts or vesicles.

Previous studies in other laboratories have provided evidence suggesting that Band III protein spans the membrane. The evidence is based on comparative analysis of radiolabeled peptide products of Band III derived from labeled intact cells and from fragmented ghosts (7) and also proteolytic digestion of Band III in inside-out vesicles as measured by Coomassie blue staining (2). The present data have substantiated and extended these earlier studies showing not only that Band III can be digested or

![Fig. 8. Protein scans of inside-out vesicles treated with trypsin.](image1)

![Fig. 9. Digestion of 131I(labeled) inside-out vesicles with varying concentrations of trypsin. The radioactivity profiles shown were obtained following digestion with trypsin added as described in Fig. 6 and then digested with varying concentrations of trypsin for 10 min at 37°C. The radioactivity profiles shown were obtained following digestion with trypsin added at: a, 0 μg/ml (control); b, 1 μg/ml; c, 2 μg/ml; d, 10 μg/ml. The ratio of 131I added (cpm) to 131I added (cpm) = 0.58.](image2)
labeled from either surface but also that digestion of Band III from one surface can affect the mobility of components labeled from the other surface. Thus pronase treatment of resealed ghosts labeled from the outer surface with 125I and the cytoplasmic surface with 35S degraded the double-labeled 100,000 molecular weight component which contained both 125I and 35S. That pronase acted only on the outer surface was indicated by its lack of effect on the 125I (inner surface)-labeled 200,000 molecular weight component. Similarly, treatment at the cytoplasmic surface of double-labeled inside-out vesicles with pronase, trypsin, and chymotrypsin resulted in each case, in the digestion of Band III as evidenced by appearance of 125I radioactivity at a lower molecular weight. Thus these experiments indicate that the 100,000 molecular weight peptide labeled from the cytoplasmic surface with 125I as well as with 35S outside must extend through the membrane.

The results have not only substantiated that Band III material spans the membrane but have also provided evidence for asymmetry and heterogeneity of this material. It has been shown previously by NH1-terminal analysis that Band III is not a single peptide but is heterogeneous (46). Not only have a number of functions including anion (30) and cation (47) transport been ascribed to the 100,000 molecular weight component have indicated heterogeneity of this material. It has been shown previously by NH1-terminal analysis that Band III is not a single peptide but is heterogeneous (46). Not only have a number of functions including anion (30) and cation (47) transport been ascribed to the 100,000 molecular weight component have indicated heterogeneity or simply sequential products of the same components in Band III.

The arrangement of Band III protein(s) in the membrane must be reconciled with some of the effects of labeling and digestion as suggested by Bretscher (7). Thus trypsin and pronase digestion of Band III at the inner surface was apparent, in both cases, as a decrease in molecular weight and as a loss of 125I radioactivity. In contrast, at the outer surface, trypsin did not digest Band III and pronase, which cleaved a 20,000 to 30,000 molecular weight fragment, removed relatively little or none of the 125I radioactivity from the outer surface; that is, the 125I:35S ratio was similar in Band III before digestion and in the major 60,000 to 70,000 dalton product after digestion. This indicates that pronase removes a large fragment which is mostly unlabeled either because it has no tyrosines which is unlikely for a large hydrophilic peptide, or because the tyrosines are inaccessible, perhaps buried within the lipid, i.e. the protein may fold back into the lipid. Similar results were obtained with small molecular weight probes, by Bretscher, using formylmethionyl sulphone methyl phosphate (11) and by Cabantchik and Rothstein using 4,4’-diisothiocyanato-2,2’-dinitrosoibene disulfonate (49).

The evidence that Band III is composed of a 100,000 molecular weight material which spans the membrane asymetrically, may have important implications when considered in relation to certain membrane functions. For example, ion and solute transport, including carrier-mediated ion and solute exchange, is characterized by interactions of specific transport proteins with ligands on both sides of the membrane. In fact, it has been shown recently that the 4,4’-diiisothiocyanato-2,2’-dinitrosoibene disulfonate-labeled anion exchange protein of the human red cell is a component of Band III (30). The (Na+, K+)-pump protein, which is characterized by 32P-labeled 93,000 molecular weight polypeptide, also belongs to the Band III “group” (47); it is activated by Na+ and hydrolizes ATP on the inside, and is activated by K+ and binds ouabain on the outside of the cell (see Ref. 1). The question remains whether a molecular weight of 100,000 molecular weight is a general characteristic of mamalian transport proteins. If so, the mechanistic significance of both the size and arrangement in the membrane of such proteins should be considered.

REFERENCES

Additions and Corrections

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In Reichstein, Esther, and Rhoda Blostein. Arrangement of Human Erythrocyte Membrane Proteins

Page 6256, first column, the Reference following the first footnote should be:

(22)

Page 6262, first column, second paragraph, line 19, should read:

From the results of proteolysis of inside-out vesicles (Fig. 9) . . .

We suggest that subscribers photocopy these corrections and insert the photocopies at the appropriate places where the article to be corrected originally appeared. Authors are urged to introduce these corrections into any reprints they distribute. Secondary (abstract) services are urged to carry notice of these corrections as prominently as they carried the original abstracts.
Arrangement of human erythrocyte membrane proteins.
E Reichstein and R Blostein


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