Characterization of Globin Messenger Ribonucleic Acids in Membrane Polysomes of Mouse Reticulocytes

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SUMMARY

Between 20 and 30% of the polysomes in mouse reticulocytes are associated with the cell membrane fraction. These polysomes are not liberated by washing with 0.5 m KCl and are therefore thought to be attached to membranes. They have the same percentage of polyadenylic acid-containing RNA, as determined by oligo(dT)-cellulose affinity chromatography, as cytoplasmic polysomes. Analysis of the RNA by polyacrylamide gel electrophoresis in aqueous solutions shows that at least 95% of the RNA migrates identically with the cytoplasmic polysomal globin mRNAs. Electrophoresis in 99% formamide resolves the membrane mRNAs into two bands which migrate identically with the cytoplasmic α- and β-globin mRNAs. The molar ratio of the α- and β-globin mRNAs, as determined by quantitating the bands on the formamide gels, is similar to that of the cytoplasmic mRNAs. There is also no difference in biological activity between the two messenger preparations. The polyadenylic acid in the membrane mRNAs, isolated after labeling mice in vivo for 20 hours with [32P]orthophosphate, migrates with the three broad size classes previously shown to be present in the cytoplasmic globin mRNAs. The [32P]specific activity of the membrane mRNAs and ribosomal RNA fractions after different times of labeling with [32P]orthophosphate is similar to those from cytoplasmic polysomes. These observations show that the reticulocyte membranes contain approximately 20% of the cellular globin mRNAs, and that these mRNAs are similar to those from cytoplasmic polysomes.

In many animal cells, polysomes exist either free in the cytoplasm or bound to the endoplasmic reticulum (1-3). Although there is evidence that free and membrane-bound polysomes synthesize different classes of protein (4-6), it is not clear whether this differential activity is a result of mRNA distribution per se or is due to other factors (7-9). Attempts to find differences between free and membrane-bound mRNAs have been unsuccessful. One possibility, that of very different sizes of poly(A) regions, has been eliminated (10, 11).

It has been reported that 20% of the polysomes in reticulocytes are membrane-bound (12-15). These polysomes may be bound to the cell membrane rather than the endoplasmic reticulum as the latter structures are not readily detectable in reticulocytes. Analysis of the membrane-bound RNA showed that it contains a 9 S RNA fraction which co-migrates with the cytoplasmic 9 S globin mRNA on 3% polyacrylamide gels (16). This RNA represents about 1% of the membrane ribosomal RNA and is not derived from the pelleted white cells (16). These preliminary studies therefore suggested that the membrane-bound polysomes contain globin mRNA-like RNA. However, it is not known what percentage of the mRNA in these membrane-bound polysomes is globin mRNA or if the globin mRNA present is identical with that found in the free cytoplasmic polysomes. The answers to these questions may be helpful in understanding the significance of the membrane-bound polysomes found in reticulocytes.

In this paper we show that 20% of total mRNA in mouse reticulocytes is located on reticulocyte membrane polysomes, and that this mRNA is identical with the free cytoplasmic polysomal mRNA in size and biological activity. The poly(A) distribution in the two mRNAs after labeling mice in vivo with [32P]orthophosphate for 20 hours was also similar.

METHODS

Isolation of Free and Membrane-bound Polysomes—Reticulocytes were collected from mice made anemic with six daily injections of phenylhydrazine hydrochloride (17, 18). The cells were washed by the method of Lingrel et al. (17, 18) and lysed by the addition of 4 volumes of 10 mM KCl, 1.5 mM MgCl2, and 10 mM Tris-HCl (pH 7.6). The membranes were removed by centrifugation at 15,000 X g for 15 min (19, 20). Free polysomes were isolated from the supernatant fraction by a further centrifugation for 3 hours at 150,000 X g. Membrane-bound polysomes were isolated by the method of Bulova and Burk (15). The membranes were washed four times with 4 volumes of lysis buffer and pelleted white cells were discarded. Polysomes were dissociated from the membranes by treatment with 0.2% sodium deoxycholate (15). After centrifuging down the membranes at 15,000 X g for 15 min, the polysomes were isolated by centrifugation at 150,000 X g for 3 hours. Isolation of 9 S RNA—RNA was isolated from free and membrane-bound polysomes by extraction with phenol-chloroformisoamyl alcohol (20-22). The polysomes were taken up in 99% formamide gels, is similar to that of the cytoplasmic mRNAs. There is also no difference in biological activity between the two messenger preparations. The polyadenylic acid in the membrane mRNAs, isolated after labeling mice in vivo for 20 hours with [32P]orthophosphate, migrates with the three broad size classes previously shown to be present in the cytoplasmic globin mRNAs. The [32P]specific activity of the membrane mRNAs and ribosomal RNA fractions after different times of labeling with [32P]orthophosphate is similar to those from cytoplasmic polysomes. These observations show that the reticulocyte membranes contain approximately 20% of the cellular globin mRNAs, and that these mRNAs are similar to those from cytoplasmic polysomes.
of phenol-chloroform-isooctyl alcohol, the phases were separated by centrifugation at 15,000 × g for 15 min at room temperature. After three extractions, the polynuclear RNA was precipitated by the addition of 2 volumes of ethanol. It was passed over an oligo-(dT)-cellulose column in 0.1 M NaCl, 0.05 M Tris (pH 7.4) (22, 23). The bound poly(A)-containing RNA was eluted with water. The RNA which was not retained by the column was ethanol-precipitated; the poly(A)-containing RNA was made 0.1 M in NaCl and again passed over the column to purify it from residual rRNA contamination (22). The hybridized RNA was eluted with water before and was then precipitated with ethanol.

Isolation of Ribosomal RNAs—The non-poly(A)-containing RNA was made 2.0 M with sodium chloride and the 18 S and 28 S RNAs were precipitated by standing overnight at 4° followed by centrifugation for 30 min at 15,000 × g.

Labeling with [32P]Orthophosphate—Anemic mice were injected on the 6th day with [32P]Orthophosphate 4 hours after the last phenylhydrazine injection (22, 23) and the reticulocytes collected after 20 hours. Polysomal mRNA was prepared as above. In each experiment, the mice were injected with [32P]Orthophosphate at different times prior to collection of reticulocytes.

Millipore Filter Fractionation—The [32P]RNA was fractionated on Millipore filters according to Brawerman et al. (24) as modified by Gorski et al. (22). Filter-bound RNA was eluted by shaking in 2 ml of H2O for 1 hour followed by a second elution with 2 additional ml of H2O (22).

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RNAse Digestion and Recovery of Poly(A) Fragments—The [32P]-mRNA fractions were digested with 1 unit each of T1 and pancreatic RNases per 20 pg of RNA for 30 min in 300 mM NaCl, 2 mM EDTA, and 20 mM Tris (pH 7.5) (22, 23). Poly(A) fragments were separated from the rest of the RNA digest by their selective retention on an oligo(dT)-cellulose column (22, 23).

Base Composition of 32P-Labeled Polynucleotides—RNA was digested with 0.33 N KOH for 18 hours at 37°, neutralized with HClO4, and lyophilized. The nucleotides were desalted by passage over a Bio-Gel P-2 column (23). The base composition was determined by high voltage paper electrophoresis (23).

Gel Electrophoresis—Cytoplasmic and membrane mRNAs were subjected to electrophoresis on sodium dodecyl sulfate 5% polyacrylamide gels (0.5 × 8 cm) according to Starynov et al. (23) as modified by Morrison et al. (20). Poly(A) fragments were electrophoresed on sodium dodecyl sulfate 12% polyacrylamide gels (22, 23). Formamide gels were prepared according to Starynov et al. (23). The 7.5% polyacrylamide gels (0.5 × 8 cm) and 10% polyacrylamide gels (0.5 × 8 cm) were run for 30 min at 1 ma per gel, then for 3 hours at 3 ma per gel (20). The formamide gels were washed in water for 4 hours, then stained with 0.2% toluidine blue for 1 hour. The gels were scanned at 260 nm in a Gilford spectrophotometer (20).

Cell-free Protein Synthesis—Messenger activity of 9 S RNA fractions was assayed in the duck reticulocyte lysate system according to Lingrel et al. (18). The globins were extracted with acid-acetone and the products were separated on carboxymethyl-cellulose (18).

RESULTS

Percentage of RNA in Membrane Polysome Fractions—When membrane-bound and free polysomes were prepared from several batches of reticulocytes, the percentage of RNA in the membrane fraction was between 15 and 23% of that in the free polysomes (Table I). The recovery of poly(A)-containing mRNA from both fractions varied between 0.9% and 1.2% of the non-poly(A)-containing RNAs (Table I). The membrane-bound polysomes therefore contained between 15 and 23% of the total cellular poly(A)-containing mRNA population.

As treatment with high salt has been shown to preferentially release those polysomes which are only loosely bound to the endoplasmic reticulum in other cell types (26, 27), the recovery of reticulocyte membrane-bound RNA was compared with or without washing in 0.5 M KCl. Only a negligible loss of RNA occurred from the membranes which were washed in high salt (Table I, Experiment 4).

**Table I**

| Experiment | Total polysomes | mRNA in polysomes |
|------------|-----------------|-------------------|
|            | Free | Membrane-bound | Free | Membrane-bound |
| 1          | 85   | 15             | 0.9  | 1.2            |
| 2          | 77   | 23             | 1.1  | 1.0            |
| 3          | 80   | 20             | 1.2  | 0.9            |
| 4          | 80   | 20             | 1.0  | 0.9            |

FIG. 1. Sodium dodecyl sulfate 3% polyacrylamide gels of membrane and cytoplasmic mRNAs. The mRNAs were isolated as outlined under "Methods." The gels were electrophoresed for 20 min at 1 ma per gel, then for 2 hours at 4 ma per gel. a, 4 μg of mRNAs from free cytoplasmic polysomes; b, 6 μg of mRNAs from membrane polysomes; c, 4 μg of membrane mRNAs + 4 μg of free cytoplasmic mRNAs.

Size Characterization of Membrane-bound mRNA—The RNAs isolated from membrane-bound polysomes migrated similarly to the globin mRNAs from cytoplasmic polysomes when they were subjected to electrophoresis on sodium dodecyl sulfate 3% polyacrylamide gels (Fig. 1, a and b). Samples of both RNAs subjected to electrophoresis on the same gel showed no greater spread in band width than did the separate samples (Fig. 1c). Scanning the unstained gels at 260 nm showed that greater than 98% of the membrane mRNA migrated in the 9 S RNA region.

Although electrophoresis in aqueous gels showed that there was negligible contamination of the membrane mRNAs by RNAs with sizes other than 9 S, the presence of mRNAs corresponding exactly in size to both α- and β-globin mRNAs could not be determined. When the membrane mRNAs were subjected to electrophoresis on 7.5% polyacrylamide gels in 99% formamide, conditions in which the cytoplasmic mRNAs are resolved into their α- and β-globin mRNA components (20), the membrane mRNAs were also resolved into two bands (Fig. 2b). The migration of these bands relative to the 4 S and 5 S RNA was the same as for the cytoplasmic mRNAs (Fig. 2a). Electrophoresis of both cytoplasmic and membrane mRNAs on the same gel (Fig. 2c) showed no broadening of the bands. By both these criteria, the membrane mRNAs migrate identically with the cytoplasmic α- and β-globin mRNAs. Fig. 3 shows a stained gel of the membrane mRNAs after electrophoresis on 10% polyacrylamide gels in the presence of formamide.

The molar ratio of β-mRNA to α-mRNA in the membrane RNA preparations was determined by scanning the stained 7.5% and 10% formamide gels at 260 nm and quantitating the area under each peak (20). The results show a molar ratio of 1.1 to...
plasmic mRNAs. Membrane polysomes; c, 3 pg of membrane mRNAs + 3 pg of cytoplasmic polysomes; b, 6 pg of mRNAs from membrane polysomes; a, 6 pg of mRNAs from free cytoplasmic polysomes. a, 6 pg of mRNAs + 3 pg of cytoplasmic mRNAs + 3 pg of cytoplasmic mRNAs + 3 pg of cytoplasmic mRNAs.

mRNAs were isolated as outlined under “Methods.” Gels were electrophoresed for 30 min at 1 ma per gel, then for 3 hours at 4 ma per gel. To each gel, along with the mRNA samples, 15 µg of 5S and 5S RNA markers were applied. a, 6 µg of mRNAs from free cytoplasmic polysomes; b, 6 µg of mRNAs from membrane polysomes; c, 3 µg of membrane mRNAs + 3 µg of cytoplasmic mRNAs.

Biological Activity—Although the size estimates show that the membrane mRNAs are very similar in size to those in the cytoplasm, they provide no information on the biological activity of the membrane mRNAs. In order to determine whether the membrane mRNAs were as active in globin synthesis as the cytoplasmic polyosomal mRNAs, both were assayed for α- and β-globin chain synthesis in duck reticulocyte lysates.

The biological activity of the membrane mRNAs was similar to that of cytoplasmic mRNAs prepared from polysomes isolated in the presence of 0.2% sodium deoxycholate (Table II). The mRNAs prepared from membranes treated with high salt showed a comparable globin synthetic activity to those prepared in the usual manner. In all cases, the mRNAs isolated from deoxycholate-treated polysomes showed approximately one-half of the globin synthetic capacity of cytoplasmic polyosomal mRNAs (Table II).

The comparable β to α-globin synthesis in both membrane and cytoplasmic fractions shows that there is no preferential accumulation of β- or α-globin mRNA activity in the membrane-bound polysomes.

Poly(A) Content of mRNAs Labeled with [32P]Orthophosphate 20 Hours before Collection of Reticulocytes—In order to compare the poly(A) content of free and membrane-bound mRNAs, mice were injected with [32P] orthophosphate 20 hours before collecting the reticulocytes, and mRNAs were prepared as under “Methods.” The distribution of the poly(A) tracts in both messenger fractions was determined by RNAse digestion followed by isolation of the poly(A) tracts and size determination on polyacrylamide gels. The base composition of the poly(A) fragment from one deoxycholate-treated membrane mRNA preparation showed that the adenine content of the poly(A) fragments was similar to that obtained when a control [3H]poly(A) was digested. Electrophoresis of the poly(A) fragments on 12% polyacrylamide gels (Fig. 4a) shows that the main size classes of poly(A) found in the mRNAs from cytoplasmic polysomes (22) are also found in the membrane mRNAs.

We have previously shown that the cytoplasmic mRNAs with different size classes of poly(A) can be fractionated on Millipore filters (22). The mRNAs containing the larger size classes, 55 to 65 and 75 to 120 nucleotides in length, are retained on the filters while the mRNAs containing poly(A) of 35 to 45 nucleotides in length do not bind to the filters. These experiments proved that the different size classes of poly(A) were found on different messenger populations and were present in both α- and β-mRNAs (22). A sample of membrane-bound mRNA which was similarly fractionated on Millipore filters showed the same poly(A) distribution between the Millipore-bound and unbound mRNAs as that shown for the cytoplasmic globin mRNAs (Fig. 46). The Millipore-bound and unbound mRNAs also have similar β-mRNA to α-mRNA ratios as determined by electrophoresis on polyacrylamide gels in the presence of formamide (results not shown). The distribution of poly(A) lengths between the two messengers is therefore similar for the cytoplasmic and membrane globin mRNAs.

Specific Activity of RNAs after Different Labeling Times—Although the chemical and biological characteristics of the mRNAs from free and membrane-bound polysomes show no difference between them, it is still possible that the membrane-bound RNAs are synthesized at different times than those in the cytoplasm. The specific activities of RNAs isolated from animals which received [32P]orthophosphate at various times prior to collection of reticulocytes were therefore examined.

When anemic animals are injected with [3P]orthophosphate, the 32P is incorporated into RNAs synthesized by all the precursor cells. Since the precursor cells only appear in the circulation when they have matured into reticulocytes, the labeled RNA present in circulating reticulocytes originates only from those

Fig. 2. The 7.5% polyacrylamide gel electrophoresis of membrane and cytoplasmic mRNAs in the presence of formamide. The mRNAs were isolated as outlined under “Methods.” Gels were electrophoresed for 30 min at 1 ma per gel, then for 3 hours at 4 ma per gel. To each gel, along with the mRNA samples, 15 µg of 4S and 5S RNA markers were applied. a, 6 pg of mRNAs from free cytoplasmic polysomes; b, 6 pg of mRNAs from membrane polysomes; c, 3 pg of membrane mRNAs + 3 pg of cytoplasmic mRNAs.

Data for Table II

| mRNA fraction | α-Globin | β-Globin | α-Globin + β-Globin |
|---------------|---------|---------|---------------------|
| Cytoplasmic 9S RNA isolated using deoxycholate | 120 | 160 | 170 |
| Membrane 9S RNA | 87 | 63 | 150 |
| Membrane 9S RNA isolated from salt-washed membranes | 81 | 70 | 151 |
| Cytoplasmic 9S RNA | 170 | 149 | 319 |
FIG. 4. Sodium dodecyl sulfate 12% polyacrylamide gels of [32P]poly(A)-containing fragments from total membrane mRNAs and Millipore-fractionated membrane mRNAs. An aliquot of the globin mRNAs labeled by injection of [32P]orthophosphate into mice 20 hours prior to collection of reticulocytes was fractionated on Millipore filters (see "Methods"). Samples of the bound, unbound, and unfraccionated RNAs were digested with RNase T1 and RNase A (see "Methods"). The poly(A)-containing fragments were isolated by oligodeoxythymidylate cellulose affinity chromatography, desalted, and lyophilized prior to electrophoresis (see "Methods"). Reticulocyte 4 S and 5 S RNAs were used as standards. a, poly(A) fragments from unfractionated mRNA; b, poly(A) fragments from Millipore-bound and unbound mRNAs. c --- c, fragments from Millipore-bound mRNA; O --- O, fragments from Millipore unbound mRNA; △ --- △, fragments from unfractionated mRNA.

cells which mature in the time interval between labeling and collection. The labeled RNA entering the circulation shortly after [32P]orthophosphate injection represents newly synthesized RNA while that entering at later times represents older RNA (22).

The specific activities of the RNAs from both free cytoplasmic and membrane-bound polysomes are very similar in the 6- to 26-hour time interval studied (Fig. 5). The specific activity of the membrane poly(A)-containing RNAs also followed that of the cytoplasmic poly(A)-containing RNAs, although some differences were noted at the 5-hour and 26-hour time points.

DISCUSSION

The membrane-bound polysomes contain approximately 20% of the total cellular poly(A)-containing mRNA. It is likely that these polysomes are truly membrane-bound as they are not dissociated by washing with high salt. This procedure has been shown to dissociate ribosomes which are loosely bound while leaving tightly bound ribosomes still attached to the membranes (25, 26).

Over 95% of the membrane-bound mRNA migrates in the 9 S RNA region on sodium dodecyl sulfate 3% polyacrylamide gels. This 9 S RNA is identical in size with the α- and β-globin mRNAs isolated from cytoplasmic polysomes as determined by electrophoresis on 7.5% polyacrylamide gels in the presence of formamide. Electrophoresis of the membrane mRNAs and marker ribosomal RNA species on 3.6% polyacrylamide gels in the presence of formamide also showed that the molecular weights of the α- and β-globin mRNAs from membranes were identical with those from the cytoplasmic polysomes.1 There is therefore no difference in the lengths of the noncoding regions between the cytoplasmic and membrane α- and β-globin mRNAs (20).

The biological activity of the membrane mRNAs is also similar to that of the free polysomal mRNAs. This result agrees with the finding that the amount and nature of the nonglobin proteins synthesized by free cytoplasmic polysomes in reticulocytes are similar to those synthesized by the membrane polysomes (28, 29). There is, therefore, no evidence for a preferential localization of nonglobin mRNAs on the membrane-bound polysomes such as proposed by Bulova and Burka (15), although our studies do not rule out the synthesis of a small amount of noneheme protein.

We have previously shown that the the molar ratio of β- and α-mRNA in the postmembrane supernatant fraction of reticulocytes is approximately 1 (20). The globin mRNA localized in the membrane polysomes also has a β:α ratio close to unity. Thus, there is no preferential localization of either messenger in the membrane fraction. The molar amounts of β- and α-mRNAs in the total cellular mRNA population is therefore close to 1.

There has been some disagreement about the synthetic products of membrane-bound polysomes. In rabbits, for example, the proteins synthesized by these polysomes do not comigrate with globin chains (15, 29). However, the tryptic peptide analysis showed that greater than 95% of the protein synthesized by the membrane-bound polysomes was globin (29). The anomalous migration of the rabbit globins may be an artifact induced by the isolation of globins synthesized by membrane-bound polysomes in cell-free systems as the globins synthesized by isolated mouse membrane globin mRNAs in a reticulocyte lysate migrate identically with mouse α- and β-globin chains.

Although our results show that approximately 20% of the

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cellular globin mRNAs are present in membrane-bound ribosomes, this does not imply that all the membrane-bound mRNAs are active in globin synthesis. Although Woodward et al. (29) found that bound ribosomes contained about 12% as much radioactivity as did free ribosomes after cells were incubated with [3H]tyrosine for 10 min, we find that approximately 20% of the total globin mRNAs are located on the membranes. Thus, it is possible that, although the isolated membrane-bound globin mRNAs are as active in cell-free systems as the cytoplasmic messengers, their activity may be modified in vivo. Such a modification of activity has been shown for ferritin mRNAs localized on membrane-bound polysomes and albumin mRNAs localized on free cytoplasmic polysomes (9).

Burka et al. (12) have suggested that the newly synthesized rRNA appears first in the free cytoplasmic polysome pool before becoming localized in the membrane polysomes. The specific activities of rRNAs in our experiments at the various times examined do not support such a scheme unless there is a rapid equilibration between free and membrane-bound polysomes either in the erythroid precursor cells in the spleen and bone marrow or in the reticulocytes newly released into the circulation. Although there are some differences between the specific activities of free and membrane-bound mRNAs at 5 and 25 hours, we are not yet sure of their significance.

The distribution of poly(A) sizes within the membrane mRNA fraction after labeling mice in vivo for 20 hours with [32P]orthophosphate is identical with that observed in the free cytoplasmic globin mRNAs. Thus, the poly(A) size is not a basis for the distribution of the mRNAs between the two polysome compartments after this time interval. It is possible that the degradation of the poly(A) regions in the membrane-bound mRNA follows a different time course from that in the cytoplasmic mRNA and experiments are in progress to further specify the activities and the poly(A) content of the mRNAs at different times. These experiments should elucidate further the role the membrane-bound mRNAs play in the regulation and processing of the reticulocyte mRNA population.

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