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ISOLATION AND PROPERTIES OF TRANSFERRIN MESSENGER RNA FROM RAT LIVER

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UDC 547.963.3

Highly purified transferrin mRNA characterized by electrophoretic and sedimentational homogeneity has been obtained from rat liver, with a sedimentation coefficient of 20S and a molecular weight of 0.86 MD. In a system consisting of a lysate of rabbit reticulocytes the Tf-mRNA programs the synthesis of an immunoreactive precursor of transferrin with a molecular weight of 82 kD. More than 50% of the nucleotide sequence of Tf-mRNA is present in the paired state.

Transferrin (Tf) is the main carrier of iron in the organism of vertebrates and is a donor of iron for such vitally important hemoproteins as hemoglobin, the cytochromes, catalase etc. Genetic anomalies in the structure and function of Tf may play an important role in the pathogenesis of such hereditary diseases as hemochromatosis and atransferrinemia. Consequently, progress in their study must be linked primarily with the existence of information on the structure of the normal Tf gene of mammals, the sequence of stages in the expression of the Tf gene, and the molecular organization and functional activity of Tf mRNA. At the same time there is no information in the literature on the molecular structure and mechanisms of the expression of the TF gene of Man and other mammals.

In the course of a number of years we have been investigating the mechanism of the expression of the transferrin gene in the rat liver. This protein is synthesized in the membrane-bound polyribosomes of the liver [1, 2] and then passed through a complex pathway of intracellular transport and post translational modification which procede the secretion of the mature protein into the bloodstream [2].

We have isolated from rat liver highly purified transferrin mRNA characterized by electrophoretic, sedimentation, and functional homogeneity. The main structural and functional characteristics of this mRNA and also the results of experiments on its reverse transcription have been described previously [3-5].

In the present paper we give details of the isolation of the Tf mRNA and some of its physicohemical parameters.

The messenger RNA coding transferrin belongs to the predominant class of mRNAs of rat liver cells. It has been shown previously that its concentration amounts to about 7000 molecules per hepatocyte [3]. In spite of such a high level of Tf-mRNA in the liver cells, the isolation and purification of transferrin mRNA is a complex task. Table 1 shows the results

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TABLE 1. Relative Amounts of Tf-Synthesizing Polysomes and Tf mRNA in Total Polysomal Preparations from Rat Liver

Experiment No.	Proportion of Tf-synthesizing polysomes, %		Amount of poly(A)$^+$-RNA in Tf-synthesizing polysomes‡, %
	according to A^*_{260}	according to RNA†	
1	1,1	0,55	1,5
2	0,9	0,40	1,8
3	0,8	0,40	1,8

*A_{260} of the immunoprecipitate/A_{260} of the total polysomes·100.
†RNA from the immunoprecipitate/RNA from the total polysomes·100.
‡Poly(A)$^+$-RNA of the immunoprecipitate/total RNA of the immunoprecipitate·100.

of three experiments on the isolation of Tf and RNA. The proportion of Tf-synthesizing polysomes is about 1% of the total polyribosome fraction. If this figure is determined from the yield of RNA on deproteination of an immunoprecipitate and referred to the initial amount of RNA in the suspension of polysomes, the fraction of transferrin polysomes amounts to 0.4-0.5% of the total fraction. It must be mentioned that on the basis of our results on the kinetics of the hybridization of $cDNA_{Tf}$ with the total polysomal RNA [3], this magnitude should be substantially higher (~4%). The low yield of Tf-synthesizing polysomes is explained by the relatively short time of incubation of the polysomes with the "primary" and "secondary" antibodies. Under these conditions there is a substantially incomplete precipitation of Tf-polysomes. However, it is undesirable to increase the time of incubation in this case since this leads to a rise in nonspecific immunoprecipitation. The amount of poly(A)-containing RNA (Tf-mRNA) in the Tf-synthesizing polysomes varied only slightly, amounting to 1.5-1.8% of the total RNA.

The isolation of the Tf-mRNA was also monitored by measuring the translational capacity of the fractions. The translation results are given in Table 2. Since the Tf-mRNA amounted to 0.04% of the total polysomal RNA, theoretically the Tf mRNA can be purified by a maximum of 2500-fold. Judging from the template activity, purification at the immunoprecipitation stage amounted to ~7-fold. The theoretical maximum at this stage is about 20 in view of the fact that approximately 4-6% of the translatable mRNA of the liver is Tf-mRNA. Chromatography on poly(U)-Sepharose permitted the transferrin mRNA to the purified 325-fold. This magnitude is substantially lower than that expected theoretically. A number of factors affecting the accurate determination of the degree of purity of the Tf-mRNA on translation in cell-free systems may be mentioned. In the first place, the inclusion of radioactive amino acids is inhibited by heparin, which it is difficult to eliminate from the preparations completely. In the second place, in the process of isolation the mRNA is subjected to some degradation, which leads to a fall in its template activity (Fig. 1). Finally, in chromatography on a column containing poly(U)-Sepharose a certain amount of poly(U) is eluted in the form of a hybrid with the poly(A) sequence of the mRNA and interferes with the translation of such mRNAs.

The final yield of template activity of the Tf-mRNA preparations was 3.6% of the total activity of the polysomal RNA. On the whole, the figures of Table 2 demonstrate a high degree of purification of the template activity of the Tf-mRNA in the process of isolation.

To determine the degree of homogeneity of the Tf mRNA preparations [^{125}I]-transferrin-mRNA was analyzed by centrifugation in a concentration gradient of sucrose (5-20%) followed by the recording of the radioactive material in each fraction as described in the Experimental part. The results of this experiment are shown in Fig. 1. The [^{125}I]-Tf-mRNA sedimented in the form of a homogeneous peak in the 20-21S zone (molecular weight 0.8-0.9 kD). Such dimensions of the Tf-mRNA agree well with the results published previously on the determination of the dimensions of rat Tf mRNA [3, 4], and also with the dimensions of chick transferrin mRNA [6]. It must be mentioned that a certain amount of radioactive material was found in the

TABLE 2. Isolation of Transferrin mRNA

Fraction	RNA, μg	Total activity, pulses/min	Specific activity, pulses/min/μg	Purification	Yield, %
Polysomal RNA	90	12 020	133	1	100
RNA from immunoprecipitation	2	1 800	900	6,8	15
Poly(A)$^+$-RNA from the immunoprecipitate	0,01	432	43 200	325	3,6

The Tf-mRNA was isolated as described in the Experimental part. Purification was determined on the basis of the specific activity and yield on the basis of the total activity.

TABLE 3. Relative Amounts of Sections of Structure in the Tf-mRNA

Experiment No.	Radioactivity of the [^{125}I]-Tf-mRNA, pulses/min		Proportion of sections of secondary structure, %
	before nuclease hydrolysis	before nuclease hydrolysis	
1	22 000	11 371	51
2	22 000	14 190	64
3	22 000	14 200	64
4	22 000	12 188	54

light zone of the gradient. This obviously consisted of degraded Tf mRNA molecules since electrophoretic analysis of the total translation product of the Tf mRNA preparation showed the presence of only one component with a molecular mass of the biosynthetic precursor of transferrin (Fig. 3).

Thus, the Tf-mRNA preparations isolated were characterized by a high degree of purity. Summarizing the results on the isolation of the Tf-mRNA the following may be observed. The length of the isolation procedure causes some degradation of the Tf-mRNA. Consequently, at the stage of the postmitochondrial supernatant the concentration of heparin must be raised to 500 μg/ml, although even then it is impossible completely to avoid the degradation of the Tf-mRNA.

In subsequent experiments to determine the molecular mass of the Tf-mRNA we used the DNA of the recombinant plasmid pRTf-14 which contains the cDNA sequence of transferrin. The total polysomal RNA was subjected to denaturing electrophoresis in 1.4% agarose gel with 6% formaldehyde followed by transfer to a nitrocellulose filter and hybridization with the plasmid pRTf DNA that had previously been labeled in the "nick-translation" reaction. As can be seen from Fig. 2, in this system a good separation of the marker 18S and 28S rRNAs takes place (track 1). The only zone of hybridization was located between the marker RNAs (track 2). The molecular weight of the hybridized RNA was 0.860 MD, which differed only slightly from the value obtained previously for highly purified transferrin mRNA [3, 4]. Some differences between these magnitudes are probably connected with different methods of denaturing the RNA and also with errors in the method of determination.

The functional homogeneity of the Tf-mRNA was determined by translation in a lysate from rabbit reticulocytes and by electrophoresis of the translation product by Laemmli's method [7] with 0.1% SDS. As can be seen from Fig. 3, the newly synthesized transferrin migrated as a single component having a molecular weight of 82 kD. This polypeptide was precipitated by antibodies to transferrin. The dimensions of the newly synthesized transferrin correspond to the biosynthetic precursor determined previously [2, 3]. Thus, the isolated mRNA was characterized by a high degree of physical and functional homogeneity.

Transport and ribosomal RNAs have a rich secondary structure which is necessary for the fulfilment of the biological functions of these RNAs. The study of the secondary structure of messenger RNAs of eucaryotes has shown that these RNAs also contain a large number of double-stranded sections in the formation of which up to 75% of the nucleotide sequences of the mRNAs is involved [8].

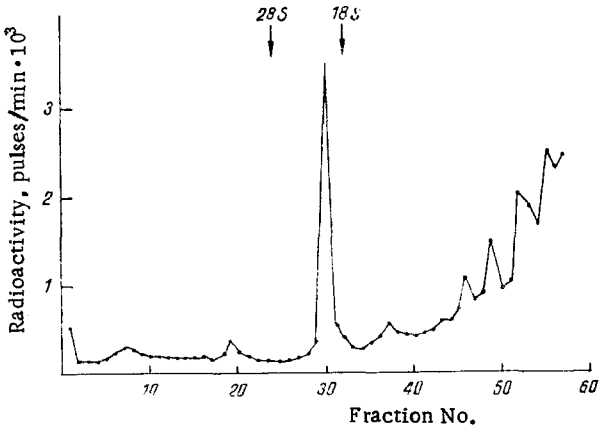

Fig. 1

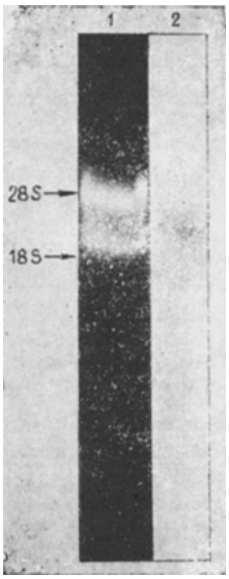

Fig. 2

Fig. 1. Sedimentation analysis of [^{125}I]Tf-mRNA in a concentration gradient of sucrose (5-10%).

Fig. 2. Determination of the molecular weight of Tf-mRNA by electrophoresis in 1.4% agarose with 6% formamide and blotting hybridization with the DNA of the plasmid pRTf labeled with ^{32}P in the "nick translation" reaction: 1) electrophoresis of the total polysomal RNA after staining with ethidium bromide; 2) hybridization of the RNA transferred from track 1 to a nitrocellulose filter with [^{32}P]pRTf-14. The arrows show the positions of 28S and 18S ribosomal RNAs.

The results of experiments to determine the relative amounts of sections of secondary structure in the Tf-mRNA molecules are given in Table 3. In these experiments a preparation of [^{125}I]Tf-mRNA was hydrolyzed with nuclease S_1 and then the radioactivity of the acid-insoluble material resistant to hydrolysis was determined. It can be seen from Table 3 that the proportion of sections of secondary structure in the Tf-mRNA amounts to 51-64% according to the results of four experiments. Approximately the same amount of sections of secondary structure has been detected for globulin mRNA [9] and ovalbumin mRNA [10].

In ceruloplasmin mRNA the proportion of paired sections is, from results on resistance to the action of a nuclease, 70-75% [11]. The dimensions of the double-stranded sections of the [^{125}I]-Tf-mRNA resistant to hydrolysis by nuclease S_1 were determined by electrophoresis in 12% polyacrylamide gel with 7 M urea [12]. The results of the electrophoresis are shown in Fig. 4. Four sections of the secondary structure of the transferrin mRNA (1-4) were detected, their dimensions being 120 n, 85 n, 35 n, and 24 n, respectively. In addition to this, a considerable amount of radioactivity remained at the start. Thus, according to the results on the resistance of [^{125}I]-Tf-mRNA preparations to the action of nuclease S_1, about 50% of the nucleotide sequences of the transferrin mRNA are present in the paired state. On electrophoretic separation under denaturing conditions, these paired sections were represented by discrete components.

On the whole, the transferrin mRNA isolated from rat liver was homogeneous according to results of sedimentation analysis and programmed the synthesis of an immunoreactive precursor of transferrin. More than 50% of the nucleotide sequence of the Tf-mRNA was present in the paired state.

EXPERIMENTAL

Transferrin was isolated from rat blood serum by a method described previously [1]. The immunization of rabbits with homogeneous preparations and the isolation of monospecific antibodies is described in the same paper. In the experiments on the immunoprecipitation of

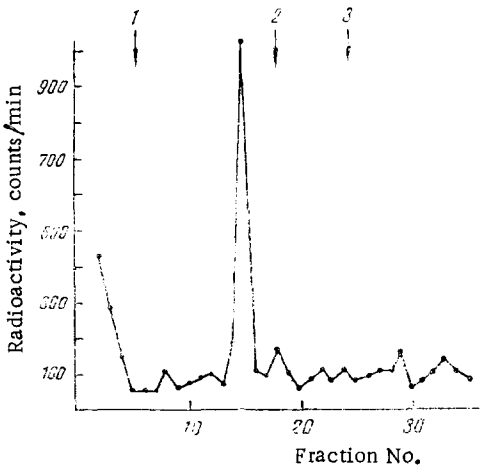

Fig. 3. Electrophoresis of the total product of the translation of purified Tf-mRNA in a cell-free system from wheat germs in 10% PAAG with 0.1% of sodium dodecyl sulfate. The arrows show the positions of the marker proteins: 1) bovine serum albumin (134 kD); 2) albumin monomer (67 kD); 3) ovalbumin (45 kD).

polyribosomes, a fraction of immunoglublins freed from RNases and proteases by chromatography on DEAE-cellulose, type 32, was used.

Isolation of the Transferrin mRNA. For the preparative isolation of the Tf-mRNA we used the basic scheme developed in the laboratory of chemical genetics of the Institute of Experimental Medicine of the Academy of Medical Sciences of the USSR for obtaining ceruloplasmin mRNA [13, 14]. Rat livers were homogenized (weight of the livers 400 g) in a buffer containing 50 mM Tris-HCl, pH 7.5, 50 mM NaCl, 5 mM $MgCl_2$, and 0.25 M sucrose with heparin (200 μg/ml). The nucleotide mitochondria were precipitated by centrifugation at 13,000 rpm in the Ty 19 rotor of a Spinco ultracentrifuge for 30 min. The supernatant was lysed with 2% Triton X-100 for 2 h, after which $MgCl_2$ was added to a concentration of 0.1 M and the mixture was left in ice for 12 h. The polyribosomes that had precipitated were purified by centrifugation through a layer of 2 M sucrose in the Ty rotor at 35,000 rpm for 20 h. The polysomes were suspended in the homogenization buffer to a concentration of 25 o.u.$_{260}$/ml. At this stage, the concentration of heparin was raised to 500 μg/ml. Antibodies to Tf were added to the suspension of polysomes in an amount of 50-60 μg/ml of suspension and the mixture was incubated at 4°C for 1 h. Then donkey immunoglobulins against the rabbit immunoglobulins were added to give a concentration 200-300 μg/ml. After 90 min, the immunoprecipitate was collected by centrifugation at 8000 rpm for 30 min. The precipitate was dissolved in a 50 mM Tris-HCl, pH 7.5, 50 mM NaCl, 5 mM $MgCl_2$ buffer, and an equal volume of 8 M urea, 8 M LiCl, 4 mM EDTA solution was added [15]. The high-molecular-weight RNA that precipitated was collected by low-speed centrifugation. The Poly(A)-containing RNA was isolated by chromatography on a column containing poly(U)-Sepharose as described by Lindberg and Persson [16]. The RNA was labeled with the isotope ^{125}I [17].

Sedimentation analysis of the [^{125}I]-Tf-mRNA. The preparation of [^{125}I]-Tf-mRNA was mixed with 5 o.u.$_{260}$/ml of total polysomal RNA (internal marker) and was deposited on a linear concentration gradient of sucrose (5-20%) prepared in a buffer containing 10 mM Tris-HCl, pH 7.6, 5 mM EDTA, and 1% sodium dodecyl sulfate [18]. Before deposition, the samples were heated at 65°C for 10 min. Then they were centrifuged in the Ty-27 rotor of a Spinco ultracentrifuge at 25,000 rpm for 4 h. The gradient was removed in fractions with the optical density and radioactivity being recorded in each fraction.

The electrophoresis of the RNA was carried out in 1.4% agarose gel containing 6% of formaldehyde [19]. The samples were heated in 98% formamide for 10 min before deposition. The electrode buffer used was a 50 mM Na phosphate buffer, pH 7.0, containing 3% of formaldehyde. Electrophoresis was performed at 150 mA per gel slab for 6 h. After the end of electrophoresis, the gel was stained with ethidium bromide (1 μg/ml) for 60 min.

The RNA was transferred to a nitrocellulose filter by Thomas' method [20]. The gel was deposited on two sheets of Whatman 3 MM paper saturated with a 20 × SSC solution. Upon the

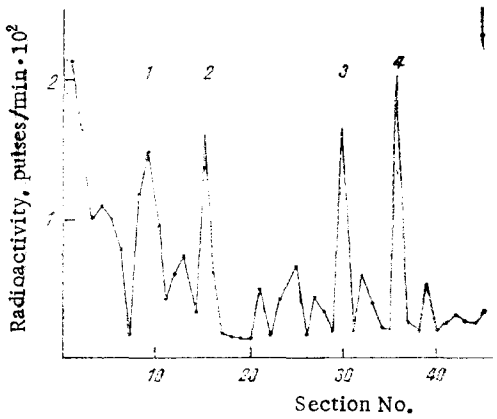

Fig. 4. Fractionation of the sections of secondary structure by electrophoresis in 12% PAAG with 7 M urea. The arrow shows the position of Bromophenol Blue.

gel was placed a sheet of Whatman 3 MM paper impregnated with the same solution and 10 sheets of filter paper. Blotting was carried out for 16 h. After transfer, the filter was dried under a lamp and was then heated in vacuum at 80°C for 2 h. The "nick translation" of the DNA of plasmid pRTf-14 and hybridization were carried out as described in [5]. The translation of the transferrin mRNA and the electrophoresis of the translation product were performed as described in [2].

Analysis of the Secondary Structure of the Tf-mRNA. The relative amount of paired sections in the transferrin RNA was determined from the resistance of preparations of [^{125}I]-Tf-mRNA to the action of nuclease S_1 [12]. The reaction was performed in an incubation system with a volume of 300 µl containing 30 mM sodium acetate, pH 4.6, 100 mM NaCl, 5% glycerol, 1 mM $ZnSO_4$, 10 µg of yeast tRNA, and 30 activity units of nuclease S_1. After incubation (30 min) the amount of TCA-insoluble radioactivity was determined. In the fractionation of the radioactivity resistant to the action of nuclease S_1, the samples after incubation were treated with an equal volume of chloroform–isoamyl alcohol (24:1). The RNA fragments were precipitated with two volumes of cold ethanol and were analyzed by electrophoresis in 12% polyacrylamide gel with 7 M urea as described by Maniatis et al. [21]. Xylene Cyanole and Bromophenol Blue (58 and 13 nucleotides in terms of mobility, respectively) were used as markers.

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SYNTHESIS OF TRITIUM-LABELED NUCLEOSIDE 5'-TRIPHOSPHATES AND NUCLEOSIDE 5'-DIPHOSPHATES

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Tritium-labeled nucleoside 5'-triphosphates (NTPs) nucleoside 5'-diphosphates (NDPs) containing the tritium label in positions 8 (in the purine nucleus) and 5 (in the pyrimidine nucleus) have been obtained by the dehalogenation of the corresponding bromine derivatives with gaseous tritium. The dehalogenation of the Br-NTPs and Br-NDPs was carried out at atmospheric pressure in an aqueous alkaline medium using palladium catalysts (5% $Pd/BaSO_4$ or α-Pd). The possibility of introducing a tritium label into nucleotides of the adenine series by the heterogeneous isotope exchange reaction with gaseous tritium in the presence of 5% $Pd/BaSO_4$ has been investigated. For the compounds synthesized, the compositions of the eluents used for the chromatographic isolation of the desired products are given. The molar activities of the compounds synthesized were between 370 and 740 TBq/mole (10-20 kCi/mole).

Tritium-labeled nucleoside 5'-triphosphates (NTPs) and nucleoside 5'-diphosphates (NDPs) are being widely used in biochemistry and molecular biology. As a rule, they are synthesized by the enzymatic phosphorylation of the corresponding labeled nucleoside 5'-monophosphates (NMPs) [1, p. 383]. However, the initial NMPs frequently have the lowest molar activity among all possible precursors (the bases, the nucleoside, the NMPs) [2, 3]. Furthermore, after the performance of the reaction the necessity arises for isolating the desired product from a complex reaction mixture containing labeled NMPs, NDPs, and unlabeled adenine 5'-triphosphate and, possibly, additional nonradioactive nucleotide material (particularly when enzyme preparations with low degrees of purification are used). In view of this, chemical methods of synthesizing tritium-labeled NTPs and NDPs based on the introduction of a tritium atom in the last stage of synthesis, which is particularly variable on working with labeled compounds, are of interest.

The aim of the present work was to obtain NPTs and NDPs containing the tritium label in positions 8 (in the purine nucleus) and 5 (in the pyridine nucleus) introduced by the dehalogenation of the corresponding bromine derivatives with gaseous tritium, for example:

$$\text{NTP} \rightarrow \text{Br-NTP} \xrightarrow[\text{Pd}]{^3H_2} [^3H]\,\text{NTP}. \quad (1)$$

In contrast to NMPs, the bromination [4, 5] and subsequent debromination [2, 3] of which have been described in detail, the corresponding information for the NTPs and the NDPs* is extremely limited [6, 7].

The bromination of purine nucleotides by the action of bromine in an acetate buffer without preliminary protection of the ribose residue was first described by Ikehara [6]. We obtained 8-Br-ATP and 8-Br-dATP under these conditions (Table 1).

*Abbreviations adopted: ATP — adenosine 5'-triphosphate; GTP — guanidine 5'-triphosphate; UTP — uridine 5'-triphosphate; CTP — cytidine 5'-triphosphate; dNTP — a 2'-deoxynucleoside 5'-triphosphate.

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