We examined the hypothesis that initiation of eukaryotic protein synthesis involves ATP-dependent melting of 5'-cap-proximal secondary structure in mRNA by eukaryotic initiation factors 4A and 4B. In reticulocyte lysate depleted of ribonucleoside triphosphates by pretreatment with hexokinase/glucose, initiation complex formation by native reovirus mRNA showed a strict requirement for ATP. The corresponding mRNA synthesized with ITP in place of CTP to minimize secondary structure also required ATP for binding to 40 S ribosomal subunits in complexes characteristic of initiation. In a partial reaction without ribosomes, purified eukaryotic initiation factors 4A and 4B bound and cross-linked to the capped 5'-end of oxidized mRNA. This interaction was ATP-dependent with inosine-substituted or bromouridine-containing reovirus RNAs as observed previously with native mRNA. The results indicate that if initiation involves ATP-dependent denaturation of mRNA, the effect must occur after initiation factor-mediated attachment of mRNA to the 40 S ribosomal subunit.

Initiation of eukaryotic protein synthesis differs from the corresponding prokaryotic process in several important ways. Among them is an ATP requirement for formation of initiation complexes consisting of mRNA bound to 40 S ribosomal subunits (1, 2). Furthermore, in contrast to the multiple internal initiations that occur in polycistronic prokaryotic messengers, most eukaryotic mRNAs initiate translation exclusively at the 5'-proximal A-U-G, i.e., near the 5'-terminal m7GpppN 'cap' (3). A scanning model has been proposed to explain 40 S subunit selection of the A-U-G closest to the 5'-end (4). In this model, 40 S subunits bind at or near the cap and reposition at the first A-U-G where Met-tRNA\(^\text{Met}\) anti-codon/A-U-G base pairing, mRNA conformational constraints, and other kinds of interactions promote joining of the 60 S ribosomal subunit. Thus, the model may also account for the enhancing effect of the cap (5) and the influence of mRNA secondary structure (6) on eukaryotic initiation.

Ribosomal subunit positioning on mRNA may involve at least transient denaturation of the template, possibly mediated by initiation factors eIF-4A and eIF-4B. Both factors are required for mRNA attachment to the 40 S initiation complex, and ATP is hydrolyzed to ADP + P, at this step in partial initiation reactions (2). In addition, purified eIF-4A and eIF-4B bind mRNA, and ATP hydrolysis is necessary for this interaction as measured by filter retention of mRNA or chemical cross-linking to the capped 5'-end of oxidized mRNA (7).

As part of an effort to define the role of cap and "cap-binding" polypeptides in initiation, we prepared ATP-depleted reticulocyte lysate and examined the effect of mRNA secondary structure on the requirements for binding to ribosomes. ATP dependence for cross-linking of purified eIF-4A and eIF-4B to oxidized mRNA was also tested with mRNA that was inosine-substituted and almost devoid of secondary structure (6, 8). In both the partial, i.e., cross-linking reaction and in nucleotide-depleted unfractonated lysate, initiation by native and inosine-substituted RNA was ATP-dependent.

**EXPERIMENTAL PROCEDURES**

**Preparation of ATP-depleted Lysate—**Rabbit reticulocyte lysate (0.8 ml, 250 A\(^2\)ml/ml) was adjusted to 4 mM Mg acetate and 2 mM glucose and incubated with 32 units of hexokinase (43 units/mg, Boehringer Mannheim) for 15 min at 30 °C. The incubated lysate was filtered through a Sephadex G-25 coarse column (8.3 x 0.7 cm) that had been equilibrated with 20 mM Hepes (pH 7.3) containing 90 mM KCI, 1 mM Mg acetate, and 1 mM dithiothreitol after treatment with 5 ml of the same solution containing 1% bovine serum albumin. Fractions of 0.3 ml were collected, and the two samples with an A\(_{260}\) ≥200 were pooled and stored in 0.1-ml aliquots in liquid N\(_2\).

**Synthesis of \("\)Methyl-labeled mRNA—**The in vitro synthesis and purification of 5'-end-labeled, native, and inosine-substituted reovirus mRNAs were described (8). 5-Bromouridine-substituted mRNA was synthesized in transcription incubation mixtures containing bromouridine triphosphate in place of UTP (6).

**mRNA-Ribosome Binding Assay—**Hexokinase-treated, gel-filtered reticulocyte lysate was made mRNA-dependent by digestion with micrococcal nuclease (160 units/ml in 1 mM CaCl\(_2\)) for 12 min at 21 °C and stopped by adjusting to 2 mM EGTA according to Pelham and Jackson (10). Ribosome binding was at 30 °C for 10 min in 25-µl incubation mixtures containing 18 µl of treated lysate, 5 mM dithiothreitol, 12 mM Hepes (pH 7.6), 108 mM K acetate, 1 mM Mg acetate, 8 µM concentration each of 20 amino acids, 0.16 mM sparsomycin, 20,000 cpm of \("\)methyl-labeled reovirus mRNA (specific activity ∼70 cpm/µg), 0.8 mM GMP(CH\(_3\))P (Sigma), and, where indicated, 1 mM ATP. Digestion with RNase A (0.5-2 µg/ml, Worthington) was at 0-4 °C for 10 min. Mixtures were diluted with 0.15 M of 20 mM Tris-HCl (pH 8) containing 90 mM KCI and 3 mM Mg acetate and layered onto 10-30% glycerol gradients for sedimentation analysis as described (11).

**Protein-mRNA Cross-linking Assay—**Periodate oxidation of \("\)methyl-labeled mRNA and chemical cross-linking to initiating eIF-4A and eIF-4B was performed as described previously (12, 13). Cross-linked proteins were analyzed by sodium dodecyl sulfate-polyacrylamide gel electrophoresis and fluorography (13). Initiation factors, purified as described (7, 14) and kindly provided by W. C. Merrick and J. Grifo (Department of Biochemistry, Case Western Reserve University School of Medicine, Cleveland, OH) contained...
no CBP II as determined by their inability (individually or mixed) to restore translation of capped mRNA in extracts of poliovirus-infected HeLa cells (13); eIF-4B contained trace amounts of CBP I as detected by cross-linking (12).

RESULTS

Reticulocyte ribosomes in non-ATP-depleted lysate were tested for the capacity to bind [3H]methyl-labeled reovirus mRNA. The incubation mixture included the nonhydrolyzable GTP analog GMPP(CH3)P but no added ATP or GTP. Under these conditions, a large fraction of the mRNA formed initiation complexes, and 27 and 40% of the input radioactivity sediments in the 40 and 80 S positions in a 10–30% glycerol gradient (Fig. 1A). Since GTP hydrolysis is required for joining of 60 S ribosomal subunits to 40 S-mRNA initiation complexes (15), the radioactivity in the position of 80 S complexes presumably was derived from 40 S complexes that were formed with endogenous GTP rather than the added nonhydrolyzable analog. To reduce or eliminate mRNA binding due to endogenous ribonucleoside triphosphates, reticulocyte lysate was pretreated with glucose and hexokinase to convert endogenous ATP (16), and indirectly GTP (17), to the corresponding nucleoside diphosphates. In the depleted lysate, mRNA binding to ribosomes was dramatically decreased in the absence of exogenous ATP, and 10% or less of the input radioactivity sediments in the position of initiation complexes (Fig. 1B). This is in agreement with the demonstrated requirement for ribosome binding of mRNA in plant and animal cell-free protein synthesizing systems (1, 2). Addition of ATP to the pretreated lysate restored mRNA binding, and in the presence of GMPP(CH3)P the resulting 40 and 80 S complexes accounted for 39 and 23% of the input radioactivity (Fig. 1C). These values are close to those obtained with untreated lysate (Fig. 1A), indicating that pretreatment with glucose and hexokinase did not significantly affect mRNA binding. Full restoration of binding was also obtained in pretreated lysate supplemented with phosphate and phosphokinase as an energy-generating system (data not shown). The apparent “leakage” of 40 S-mRNA complexes to the 80 S level in the presence of GMPP(CH3)P and ATP (Fig. 1C) presumably was due to formation of GTP from residual GDP via transphosphorylation by endogenous nucleoside diphophate kinase, an activity reported earlier in reticulocyte lysates (17).

Previously, it was demonstrated for several species of reovirus mRNA that association with 40 S ribosomal subunits in authentic initiation complexes resulted in protection of both the mG cap and adjacent 5′-proximal sequence against RNase digestion (18). At the 80 S level, a subset of the 5′-sequence including the initiator A-U-G remained protected, but the cap was released by RNase digestion. To establish that the 40 S-mRNA initiation complexes formed in the ATP-depleted lysate were authentic, they were tested for resistance to degradation by RNase A. Radiolabeled mRNA was incubated in pretreated lysate containing added ATP and GMPP(CH3)P as in Fig. 1C and digested with RNase before gradient sedimentation. As shown in Fig. 1D, under these conditions there was little radioactivity associated with 80 S ribosomes, indicating that the cap in 80 S-mRNA initiation complexes was not protected. In contrast, more than 97% of the 40 S-bound radioactivity relative to an undigested control was RNase-resistant, consistent with the formation of functional 40 S-mRNA initiation complexes in the pretreated lysate.

Messenger RNAs with diminished intranuclear base pairing were found to have a lower dependence on ATP for initiation complex formation in wheat germ extract (8, 19). It was suggested subsequently that ATP is required for actively “melting” 5′-proximal secondary structure to facilitate mRNA binding to 40 S ribosomal subunits during initiation of translation (20, 21). Reovirus mRNA can be synthesized with inosine in place of guanosine, and the resulting mRNAs have greatly diminished secondary structure (6, 8). To determine if such denatured mRNAs can form initiation complexes in reticulocyte lysate in the absence of ATP, [3H]methyl-labeled, inosine-substituted reovirus mRNA was tested in the ATP-depleted system. In the presence of GMPP(CH3)P but without added ATP, 34% of the input radioactivity sedimented in the 40 S region of the gradient (Fig. 2A). This finding is consistent with previous results obtained with inosine-substituted mRNA and wheat germ ribosomes (6, 8), and may indicate that in the absence of ATP, 40 S subunits attach to denatured mRNA but cannot reposition at the correct initiation site or that the RNA forms rapidly sedimenting complexes with protein(s) under these conditions (6). In reticulocyte lysate complexes formed by inosine-substituted mRNA in the absence of ATP differed markedly from authentic 40 S-mRNA complexes and were almost completely sensitive to digestion by low levels of RNase (Fig. 2B). Furthermore, binding of inosine-substituted mRNA was increased in the presence of ATP (Fig. 2C); 23% of the input radioactivity was recovered in the 40 S region and 35% in faster sedimenting complexes. In addition to 80 S complexes, the latter may include mRNA attached to multiple 40 S subunits as described for wheat germ (6). The authenticity of the complexes formed by inosine-substituted mRNA in the presence of added ATP is suggested by their relative resistance to RNase digestion (Fig. 2D) as compared to the nuclease sensitivity of complexes formed in the absence of ATP (Fig. 2B).

![Fig. 1. Binding of reovirus mRNA to ribosomes in reticulocyte lysates.](http://www.jbc.org/Downloaded from http://www.jbc.org/ by guest on March 31, 2020)
Translation Initiation by Denatured mRNA Is ATP-dependent

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The effect of m'GMP on mRNA-ribosome complex formation was assayed as another measure of correct initiation. As shown in Fig. 3A, 1 mM m'GMP decreased ribosome binding of native mRNA by about 3-fold in pretreated reticulocyte lysate in the presence of ATP. This is readily seen from the increase in unbound radioactivity at the top of the gradient, from 40 to 81% of the input. By contrast, in the absence of ATP the formation of complexes by inosine-substituted mRNA was essentially unaffected by the addition of the cap analog (Fig. 3B). This result is consistent with the finding that most of the inosine-substituted mRNA-40 S complexes formed in the absence of ATP were sensitive to RNase and apparently not authentic initiation complexes. In the presence of ATP, ribosome binding of inosine-substituted mRNA in pretreated lysate was sensitive to m'GMP (Fig. 3C). The cap analog diminished mRNA-ribosome complex formation, and the unbound radioactivity increased from 42 to 75% of the input, i.e. similar to the effect on native mRNA.

For either RNase protection by ribosomes or cap analog inhibition of mRNA binding, AMPP(CH2)P could not substitute for ATP, consistent with a requirement for hydrolysis (data not shown). These results demonstrate that in reticulocyte lysate ATP is required for ribosome binding of either native reovirus mRNA or the corresponding inosine-substituted mRNA to form structures with characteristics of initiation complexes.

It was of interest to determine if this ATP requirement was also maintained with denatured mRNA in a partial initiation reaction involving interaction of purified factors eIF-4A and eIF-4B with mRNA in the absence of ribosomes. Factor-mRNA complex formation can be monitored by nitrocellulose filter retention (7) or by cross-linking of the proteins to the 5'-end of [3H]methyl-labeled, periodate-oxidized mRNA (12). As reported earlier (7), cap-specific cross-linking of native reovirus mRNA to eIF-4A and eIF-4B requires ATP and Mg2+ and differs from the ATP-independent cross-linking observed with the 24,000-Da cap-binding protein, CBP I (7, 12, 13, 20-22). Inosine-substituted, 5'-end-labeled reovirus mRNA was periodate-oxidized and tested for cross-linking to eIF-4A and eIF-4B in the absence and presence of ATP. Without ATP, radioactivity was associated with CBP I which is present in trace amounts in purified eIF-4B (12); no radioactively labeled band indicative of cross-linking was present in the position of eIF-4A (M, ~ 46,000), and eIF-4B (M, ~ 80,000) was weakly

Fig. 2. Ribosome binding of inosine-substituted reovirus mRNA in ATP-depleted reticulocyte lysate. Inosine-substituted, [3H]methyl-labeled reovirus mRNA was incubated in hexokinase/glucose-treated reticulocyte lysate in the presence of 0.8 mM GMPP(CH2)P (A) and analyzed as described in the legend to Fig. 1. For C and D, incubation mixtures also contained 1 mM ATP; for B and D, samples were treated with 0.5 pg/ml of RNase A as described under "Experimental Procedures." The effect of m'GMP on mRNA-ribosome complex formation was assayed as another measure of correct initiation. As shown in Fig. 3A, 1 mM m'GMP decreased ribosome binding of native mRNA by about 3-fold in pretreated reticulocyte lysate in the presence of ATP. This is readily seen from the increase in unbound radioactivity at the top of the gradient, from 40 to 81% of the input. By contrast, in the absence of ATP the formation of complexes by inosine-substituted mRNA was essentially unaffected by the addition of the cap analog (Fig. 3B). This result is consistent with the finding that most of the inosine-substituted mRNA-40 S complexes formed in the absence of ATP were sensitive to RNase and apparently not authentic initiation complexes. In the presence of ATP, ribosome binding of inosine-substituted mRNA in pretreated lysate was sensitive to m'GMP (Fig. 3C). The cap analog diminished mRNA-ribosome complex formation, and the unbound radioactivity increased from 42 to 75% of the input, i.e. similar to the effect on native mRNA. For either RNase protection by ribosomes or cap analog inhibition of mRNA binding, AMPP(CH2)P could not substitute for ATP, consistent with a requirement for hydrolysis (data not shown). These results demonstrate that in reticulocyte lysate ATP is required for ribosome binding of either native reovirus mRNA or the corresponding inosine-substituted, denatured mRNA to form structures with characteristics of initiation complexes.

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Fig. 3. Effect of m'GMP on ribosome binding of native and inosine-substituted mRNAs. Binding assays were performed in the presence (●) or absence (○) of 1 mM m'GMP with native or inosine-substituted, [3H]methyl-labeled reovirus mRNA and ATP-depleted reticulocyte lysate in mixtures containing 0.8 mM GMPP(CH2)P. A, native mRNA + 1 mM ATP; B, inosine-substituted mRNA; C, inosine-substituted mRNA + 1 mM ATP.

Fig. 4. ATP requirement for cross-linking eIF-4A and eIF-4B to oxidized mRNA. [3H]Methyl-labeled reovirus mRNAs containing inosine in place of guanosine (A) or bromouridine in place of uridine (B) were periodate-oxidized and incubated with eIF-4A (1.7 μg) and eIF-4B (5 μg in A and 2.5 μg in B) in the absence (lanes 1 and 2) or presence (lanes 3 and 4) of 1 mM ATP and 3 mM Mg acetate. Samples in lanes 2 and 4 also contained 1 mM m'GDP. Incubation conditions, reduction with NaBH4CN, polyacrylamide gel electrophoresis, and fluorography were as described (12, 13).
labeled (Fig. 4A, lane 1). Addition of ATP to the incubation mixture resulted in cross-linking of mRNA to eIF-4A and an enhanced labeling of eIF-4B (Fig. 4A, lane 3). ATP-dependent cross-linking of the initiation factors was cap-specific, i.e. cap analog-inhibited (Fig. 4A, lane 4), as defined previously for CBP I (Ref. 12 and Fig. 4A, lane 2). Reaction of eIF-4A and eIF-4B was decreased by 64 and 57%, respectively, by mGDP, as determined by comparative densitometry of lanes 3 and 4. The polypeptide component that corresponds to eIF-4F in purified eIF-4F (23) also cross-linked to inosine-substituted mRNA in the presence but not in the absence of ATP (data not shown). Cross-linking to 5-bromouridine-substituted mRNA, which contains more stable secondary structure than native mRNA (6), also required ATP (Fig. 4B, compare lanes 3 and 1) and was diminished but to a lesser extent by mGDP (Fig. 4B, lane 4). Thus, reovirus mRNA containing either more or less ordered structure than the corresponding native mRNA maintained an ATP requirement for binding and cross-linking to eIF-4A and eIF-4B.

**DISCUSSION**

Several reports on the effect of mRNA secondary structure and possible relationship to the requirement for ATP hydrolysis during initiation of eukaryotic protein synthesis have been based on mRNA cross-linking to reticulocyte-derived initiation factors (7, 13, 21, 22) and mRNA binding to wheat germ ribosomes (6, 8, 20, 21). In the present study, we compared mRNA attachment to factors and ribosomes using homologous rabbit reticulocyte components. Specifically, we examined the role of ATP hydrolysis in initiation to determine if ATP is required for active melting of mRNA by eIF-4A and eIF-4B. These polypeptides bind to mRNA and can be cross-linked to the 5'-end of capped mRNA in an ATP-dependent process (7).

In apparent contrast to wheat germ extract (8, 19), reticulocyte lysate could not be rendered dependent on exogenous ribonucleoside triphosphates simply by replacing ATP with the nonhydrolyzable analog AMP(Chp)P. However, after preincubation with heparin and glycerol followed by gel filtration, the lysate required addition of nucleoside triphosphates for initiation by native reovirus mRNA. Authentic binding as defined by 40 S subunit protection of 5'-capped sequences against RNase digestion and by mGMP inhibition was obtained in the presence but not in the absence of ATP. RNA that was synthesized with ITP in place of GTP and consequently was denatured (6, 8) was apparently capable of attaching to 40 S subunits to some extent in the absence of ATP. However, the structures were neither RNase-resistant nor -sensitive to cap analog inhibition. These characteristics of initiation complexes were acquired by inosine-substituted RNA bound to ribosomes in the presence of ATP. The results suggest that during initiation in a mammalian cell-free translating system, ATP hydrolysis is necessary for event(s) other than, or in addition to, denaturation of mRNA.

Cross-linking studies with eIF-4A and eIF-4B purified from reticulocytes support the results of the ribosome binding experiments. Unlike CBP I, association of these two initiation factors with mRNA and their cross-linking to oxidized 5'-termini requires the presence of ATP. The same requirement was observed with inosine-substituted, i.e. melted RNA or with bromouridine-containing RNA that apparently is more structurally ordered than native reovirus mRNA (6). Lee et al. (21) have reported that reticulocyte polypeptides of the same apparent molecular weights as eIF-4A and eIF-4B can be cross-linked to oxidized native mRNA in an ATP-dependent reaction. By contrast, inosine-substituted RNA was cross-linked to M, ∼ 50,000 and 80,000 polypeptides in the unfraccionated ribosomal salt wash in the absence of ATP. It was suggested that accessory factors in the crude salt wash that are ATP-dependent, RNA unwinding proteins facilitate binding of 40 S ribosomal subunits to the 5'-end of mRNA. However, the present findings with eIF-4A and eIF-4B do not support this hypothesis because ATP and the purified factors were sufficient to obtain cross-linking of these polypeptides to the 5'-cap of oxidized reovirus mRNAs, including bromouridine-substituted RNA. Furthermore, in both the partial reaction with purified factors and in the complete, but nucleotide-depleted lysate, ATP is required not only for initiation on native mRNA but also for polypeptide cross-linking and authentic ribosome binding by denatured (inosine-substituted) RNA.

These findings suggest that the interaction of eIF-4A and eIF-4B with mRNA is ATP-dependent irrespective of mRNA secondary structure. Base pairing in the 5'-region of native mRNA may influence initiation at the level of 40 S ribosomal subunit movement during positioning on the template at the initiator A-U-G (19). However, if initiation does involve ATP-dependent denaturation of mRNA, melting may occur concomitantly with 40 S ribosomal subunit migration from entry site to initiator codon but probably not before or during subunit attachment to mRNA by initiation factors.

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