The Major Messenger Ribonucleoprotein Particle Protein p50 (YB-1) Promotes Nucleic Acid Strand Annealing* 

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p50, a member of the Y-box binding transcription factor family, is tightly associated with eukaryotic mRNAs and is responsible for general translational regulation. Here we show that p50, in addition to its previously described ability to melt mRNA secondary structure, is capable of promoting rapid annealing of complementary nucleic acid strands. p50 accelerates annealing of RNA and DNA duplexes up to 1500-fold within a wide range of salt concentrations and temperatures. Phosphorylation of p50 selectively inhibits DNA annealing. Moreover, p50 catalyzes strand exchange between double-stranded and single-stranded RNAs yielding a product bearing a more extended double-stranded structure. Strikingly, p50 displays both RNA-melting and annealing activities in a dose-dependent manner; a relatively low amount of p50 promotes formation of RNA duplexes, whereas an excess of p50 causes unwinding of double-stranded forms. Our results suggest that the alteration of nucleic acid conformation is a basic mechanism of the p50-dependent regulation of gene expression.

Over the past decade, an increasing number of multifunctional proteins have been described that are involved in regulation of gene expression at both transcriptional and post-transcriptional levels (1–4). For example, proteins of the Y-box family, originally discovered in connection with their ability to bind to the Y-box promoter element, play an important role in transcriptional regulation of a wide variety of genes, in DNA repair and replication as well as in the regulation of mRNA translation, storage, and localization (5–8). These proteins represent a highly conserved group of nucleic acid-binding proteins present in bacteria, plants, and animals (9, 10). The fact that such a diversity of biological functions is displayed by closely related or even identical Y-box proteins (~98% amino acid identity between rabbit p50 and EF1α/dbpB/YB-1 from chicken, rat, and human) suggests similar mechanisms of their action. Studies to date indicate that Y-box proteins may prevent nucleic acid secondary structure formation by a mechanism that is not well understood (11–15).

p50 was described initially as the major core protein of messenger ribonucleoprotein particles (mRNPs)1 in somatic cells (11, 16–18). It is a predominant component of inactive free mRNPs. p50 content in free mRNPs is approximately 2-fold higher than that in active polysomal mRNPs (8, 19). Consistent with these data, low levels of p50 (~10 molecules/globin mRNA) stimulate translation initiation in vitro, whereas doubling of p50 amounts (~20 molecules/globin mRNA) results in complete inhibition of protein synthesis (18, 20–22). Several lines of evidence indicate that p50 is a major general translation regulator through mRNA structural arrangements and packaging (6, 8, 14, 23). First, it is found in association with a wide range of mRNAs and displays little or no sequence-specificity. Second, it possesses the strongest affinity for mRNA as compared with other mRNA-binding proteins. Third, it is capable of self-oligomerization, suggesting possible mRNA packaging when p50 is present in mRNPs in high copies. Finally, p50 was demonstrated to efficiently melt mRNA secondary structure (11).

Here, we report that p50 is able to promote the rapid annealing of complementary RNA and DNA strands and to catalyze the strand exchange between ds- and ssRNAs yielding a product with a more extended ds structure. Interestingly, the DNA annealing activity can be regulated specifically by phosphorylation of p50 by casein kinase II. Based on these results, we propose that members of the Y-box family regulate gene expression at the transcription and translational level because of their ability to modulate RNA and DNA secondary structure.

EXPERIMENTAL PROCEDURES

Materials—Restriction enzymes, RNasin, Fermentas (Viilnus) and T7 RNA polymerase used in this study were obtained from MBI. T4 polynucleotide kinase and casein kinase II were purchased from New England BioLabs. Proteinase K, NTPs, and dNTPs were from Roche Molecular Biochemicals. [α-32P]UTP (2000 Ci/mmol) and [γ-32P]ATP (5000 Ci/mmol) were from Radioisotop (Moscow). pSP72 and pSP73 vectors were obtained from Promega, and Bluescript II SK(−) was from Stratagene.

p50 Purification and Phosphorylation—Rabbit recombinant p50 was expressed in Escherichia coli BL21(DE3) and purified as described previously (22, 24). p50 was stored in buffer containing 10 mM Hepes-KOH, pH 7.6, 100 mM KCl at -70 °C. Protein concentration was determined by staining with a Micro-BCA kit (Pierce). Phosphorylation of p50 (20 μg, 0.6 nmol) was performed in a 40-μl reaction mixture containing 10 mM Hepes-KOH, pH 7.6, 5 mM MgCl2, 100 mM KCl, 2 mM dithiothreitol, 2% glycerol, 1 mM ATP using 200 units of CKII. The reaction mixture was incubated

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1 The abbreviations used are: mRNP, messenger ribonucleoprotein particle; hnRNP, heterogeneous nuclear ribonucleoprotein particle; ssRNA, single-stranded RNA; ssDNA, single-stranded DNA; dsRNA, double-stranded RNA; dsDNA, double-stranded DNA; nt, nucleotide; bp, base pair(s); PIPES, 1,4-piperazine diethanesulfonic acid; TBE, Tris-borate.
FIG. 1. p50 displays strong RNA annealing activity. Upper panels, schematic representation of the RNA annealing assay. A, annealing of the 18-bp RNA duplex. 32P-labeled 58-nt RNA (0.5 pmol) and 69-nt RNA (0.7 pmol) were incubated at 30 °C for 20 min with 0, 1.4, 2.8, 5.5, 11, and 22 pmol of p50 (lanes 1–6). Lane 7, duplex RNA obtained by hybridization of the corresponding ssRNAs in the absence of p50; lane 8, 32P-labeled 58-nt RNA alone was incubated in the presence of 22 pmol p50. B, annealing of the 85-bp RNA duplex. 32P-labeled 97-nt RNA (0.3 pmol) and 98-nt RNA (0.5 pmol) were incubated at 30 °C for 20 min with 0, 0.28, 0.57, 1.1, 2.2, or 4.5 pmol of p50 (lanes 1–6). Lane 7, duplex RNA obtained by hybridization of the corresponding RNA strands in the absence of p50. The positions of ss- and duplex-containing RNAs are indicated; the stars mark the 32P-labeled strand.

FIG. 2. The effect of temperature, salt condition, and p50/RNA stoichiometry on RNA annealing. A, 32P-labeled 58-nt RNA (0.5 pmol) and 69-nt RNA (0.7 pmol) possessing the 18-bp complementary region were incubated for 20 min with increasing amounts of p50 at 20, 30, and 37 °C. B, p50 (11 pmol) was incubated as described in A in the presence of varying concentrations of KCl at 30 °C. C, 32P-labeled 58-nt RNA (0.5 pmol) and 69-nt RNA (0.7 pmol) were incubated in the presence of the indicated concentration of MgCl2 without and with p50 at 30 °C for 20 min. 5.5 pmol (D) or 11 pmol (E) of p50 was incubated as described in A at 30 °C for the indicated times. The positions of ss- and duplex-containing RNAs are shown. In C, the longer exposure time reveals slowly migrating RNA complexes.
for 40 min at 30 °C, stopped by the addition of EDTA to 5 mM, and dialyzed against 10 mM Hepes-KOH, pH 7.6, 100 mM KCl.

Preparation of RNA and DNA Substrates—ssRNAs were produced by in vitro transcription from the T7 promoter of the appropriately linearized pSP72 and pSP73 vectors containing the same linker region in opposite orientations. Briefly, the partially complementary 58- and 69-nt ssRNAs capable of forming the 18-bp heteroduplex were transcribed from Bsu3I-linearized pSP73 and PstI-linearized pSP72, respectively. 97- and 98-nt ssRNAs bearing the 85-nt complementary region were synthesized from BglII-linearized pSP73 and XhoI-linearized pSP72, respectively. To generate dsRNAs, these two pairs of partially complementary ssRNAs were incubated in 30 mM Pipes, pH 6.8, 1 mM EDTA at 100 °C for 5 min and slowly cooled down to 20 °C. To monitor the reaction efficiency, one ssRNA of each pair was uniformly labeled with [γ-32P]ATP upon synthesis.

Complementary DNA strands used in DNA annealing reactions were obtained by polymerase chain reaction amplification of pBluescript SK(−) polylinker region using T3 and T7 universal primers. The 164-mer obtained by polymerase chain reaction amplification of pBluescript was linearized by 5′-3′ end-labeling using T4 polynucleotide kinase. To obtain ssDNAs, 164-bp DNA was denatured by heating to 95 °C for 5 min and then rapidly chilled on ice.

Assay—For RNA annealing, each ssRNA pair was mixed with increasing amounts of p50 as indicated in the figure legends. The reaction mixture (10 μl) containing 20 mM Hepes-KOH, pH 7.6, 50 mM KCl, and 0.2 units/μl RNasin was incubated at 30 °C for 20 min (unless stated otherwise). The reaction was stopped by the addition of 10 μg proteinase K, 0.1% SDS followed by incubation for an additional 5 min and then by phenol-chloroform extraction. Reaction products were separated by 5% SDS-polyacrylamide gel electrophoresis (29:1 acrylamide: bisacrylamide) in 0.5× Tris borate-EDTA at 25 mA for 2 h and visualized by autoradiography.

RNA strand exchange activity of p50 was analyzed as described above using an annealed product of nonlabeled 69-nt RNA and [32P]-labeled 58-nt RNA (containing 18-bp-long duplex), and 97-nt ssRNA possessing a 46-nt region complementary to the labeled strand of the duplex. The mixture was incubated at 37 °C for 30 min.

DNA annealing activity of p50 was analyzed as described above using the heat-denatured 5′-end-labeled 164-mer DNA. The DNA products were separated on 8% SDS-polyacrylamide gel and visualized by autoradiography. Quantification of the relative amounts of ss- and dsRNA/DNA was done using the Kodak Digital 1D Program.

RESULTS

p50 Exhibits RNA Strand Annealing Activity—RNA annealing activity was reported earlier for several proteins implicated in structural organization of heterogeneous nuclear RNA (25–29). To test whether p50 exhibits RNA annealing activity, we incubated two pairs of ssRNAs (58/69-nt and 97/98-nt long) with p50 (see “Experimental Procedures”). In both cases, the addition of increasing amounts of p50 resulted in a gradual decrease of ss-form content (Fig. 1, A and B, lanes 1–6). This was accompanied by the appearance of a predominant slowly migrating band corresponding to a duplex-containing form, which can be obtained by a standard annealing of the ssRNAs in the absence of p50 (Fig. 1, A and B, lane 7). Interestingly, the p50 annealing efficiency in the two cases was different: annealing of a pair of smaller RNAs with a short (18-nt) complementary region was completed at p50/RNA molar ratios of ~10; whereas complete annealing of longer RNAs with a longer (85-nt) complementary region was achieved at p50/RNA molar ratios of ~6 (p50/nucleotide ratios of 1.7 and 1.17, respectively). Because the p50 binding efficiency is similar for all four of ssRNAs used (data not shown), we conclude that extension of the complementary region facilitates p50 RNA annealing efficiency.

To optimize annealing conditions, RNA duplex formation was analyzed at various salt concentrations and temperatures. As seen in Fig. 2A, the ability of p50 to anneal RNA is strongly dependent on the incubation temperature; ~4-fold more p50 was required for complete annealing at 20 °C than at 37 °C. The p50 RNA annealing ability was similar at KCl concentrations from 50 to 200 mM but clearly decreased at 400 mM KCl (Fig. 2B). As expected, ATP had no effect on the reaction (data not shown), because p50 possesses no ATPase activity.2 Physiological Mg2+ concentration (1 mM) does not affect p50 anneal-

2 V. M. Evdokimova and M. A. Skabkin, unpublished data.

FIG. 3, p50 promotes renaturation of DNA strands. A, schematic representation of the DNA annealing assay. B, [32P]-labeled 164-mer heat-denatured DNA (55 fmol) was incubated in the presence of 5.5, 11, and 22 pmol of p50 (lanes 1–3) at 30 °C for 20 min. C and D, [32P]-labeled 164-mer heat-denatured DNA was incubated in the presence of 22 pmol of p50 (C) or without p50 (D) for the indicated time. The positions of heat-denatured and renatured DNA are indicated; the stars mark the [32P]-labeled strand.
ing efficiency; however, high Mg\(^{2+}\) concentration (9 mM) caused considerable RNA aggregation in the presence of p50 (Fig. 2C).

The rate of annealing was strongly dependent on the p50 concentration in the reaction mixture; a 2-fold rise in p50 concentration resulted in a decrease of a half-annealing time from the initial 20 min to 3 min (Fig. 2, D and E). In contrast, the efficiency of self-annealing of the RNAs in the absence of p50 was lower than 50% over the 24-h incubation period (data not shown). Thus, p50 accelerates RNA strand annealing up to 1000-fold in a concentration-dependent manner within a wide range of salt concentrations and temperatures.

**Stimulation of DNA Annealing by p50**—Because p50 is able to bind a broad spectrum of DNAs (8, 11), it was interesting to determine whether p50 promotes DNA annealing as well. For this purpose, complementary 164-nt-long single-stranded DNAs were obtained by heat denaturation of a labeled polymerase chain reaction product (see “Experimental Procedures”; Fig. 3, A and B). It is important to note that complete renaturation of DNA was achieved at the p50/ssDNA molar ratio of \(-600\) (p50/nucleotide ratio of 3.5), which is significantly higher than required for RNA annealing. This difference is probably because of a lower affinity of p50 for DNA than for RNA.\(^3\) The rate of p50-promoted DNA annealing was not affected significantly by the addition of ATP/Mg\(^{2+}\) by or changes in ionic strength (0–100 mM KCl) (data not shown). Remarkably, in the presence of 22 pmol of p50 at 30 °C, the half-time of DNA renaturation was 5 min, whereas without p50 this value was higher than 120 h (Fig. 3, C and D). Thus, p50 accelerates DNA annealing up to 1500-fold.

**p50 Displays Both RNA Annealing and Melting Activities in a Dose-dependent Manner**—The RNA annealing activity of p50 is surprising in the light of previous findings that high p50/RNA ratios cause RNA melting (11). Therefore, we hypothe-

\(^3\) M. A. Skabkin, V. A. Ustinov, V. M. Evdokimova, J. W. B. Hershey, and L. P. Ovchinnikov, manuscript in preparation.
sized that p50 can display either annealing or melting activity depending on the p50/RNA ratio. To test this assumption, a 69-nt RNA with predicted 55% intrastrand complementarity was used. The mobility of this native form appeared to be lower than that of the same RNA after heat denaturation (Fig. 4, lanes 1 and 6). Upon the addition of increasing amounts of p50, native RNA was converted almost completely to a faster migrating, denatured form (compare lanes 2–4 with 5 and 6). Alternatively, the addition of 11 pmol of p50 to the heat-denatured RNA resulted in its complete renaturation (compare lanes 6 and 7 with 8 and 9). Upon a further 2-fold increase of p50, the renatured natively behaving RNA was partially converted back into its denatured form as expected (lane 10). These results strongly suggest that p50 can shift the equilibrium between ss- and dsRNA forms either way in a dose-dependent manner.

*p50 Exhibits RNA Strand Exchange Activity and Promotes the Formation of the Most Extended Duplex.*—Because p50 promotes transitions between ss- and dsRNAs, we tested p50 for RNA strand exchange activity. Such an activity, reported earlier (30–32) for several proteins possessing nucleic acid strand-annaeling properties, results in the replacement of one strand in the RNA duplex with a new strand, yielding a more extended duplex. We tested the ability of p50 to facilitate the exchange of one strand in an 18-bp duplex-containing RNA for another one, a 97-nt strand that yields a 46-bp duplex (Fig. 5). The formation of a new 46-bp product was monitored by the appearance of a new band with a lower electrophoretic mobility. As seen in Fig. 5, p50 efficiently catalyzed RNA strand exchange and promoted the formation of the 46-bp duplex RNA (compare lanes 1 and 2–8). It is important to note that p50 induced only formation of a more extended duplex structure (the reverse reaction did not occur; results not shown), suggesting that the RNA strand exchange reaction is thermodynamically driven by complementary base-pairing.

**Effect of p50 Phosphorylation on Its RNA and DNA Annealing Activities.**—p50 and other Y-box proteins readily undergo phosphorylation by casein kinase II in a variety of cells (18, 33, 34). To test the effect of p50 phosphorylation by casein kinase II on its ability to accelerate RNA and DNA annealing, p50 was exhaustively phosphorylated in vitro by casein kinase II (2.6 mol of phosphate/mol of p50). Surprisingly, the phosphorylation of p50 produced no effect on RNA annealing (Fig. 6A), although it notably inhibited DNA annealing (Fig. 6B). Indeed, the addition of 22 pmol of nonphosphorylated p50 caused complete DNA annealing, whereas the same amount of phosphorylated p50 resulted in annealing of only one-third of the initial ssDNA. These results indicate that phosphorylation by casein kinase II may play a role in the p50-dependent pathway of regulation of DNA conformation.

**DISCUSSION**

In this paper we demonstrate that p50, a general component of mRNPs in mammalian cells, promotes annealing of the comple-
The effect of p50 phosphorylation by casein kinase II on RNA/DNA annealing efficiency.

A. $^{32}$P-labeled 58-nt RNA (0.5 pmol) and 89-nt RNA (0.7 pmol) possessing the 18-bp complementary region were incubated with increasing amounts of either nonphosphorylated (lanes 1–3) or phosphorylated p50 (lanes 4–6) at 30°C for 20 min. Lanes 1 and 4, 2.8 pmol; lanes 2 and 5, 5.5 pmol; lanes 3 and 6, 11 pmol of p50 was added. The positions of ss- and duplex-containing RNAs are indicated. B. $^{32}$P-labeled 164-mer heat-denatured DNA (35 fmol) was incubated with increasing amounts of either nonphosphorylated (lanes 1–3) or phosphorylated (lanes 4–6) p50 at 30°C for 20 min. Lanes 1 and 4, 5.5 pmol; lanes 2 and 5, 11 pmol; lanes 3 and 6, 22 pmol of p50 was added. The positions of the heat-denatured and renatured DNA are indicated.

Effect of p50 phosphorylation by casein kinase II on RNA/DNA annealing efficiency. A, $^{32}$P-labeled 58-nt RNA (0.5 pmol) and 89-nt RNA (0.7 pmol) possessing the 18-bp complementary region were incubated with increasing amounts of either nonphosphorylated (lanes 1–3) or phosphorylated p50 (lanes 4–6) at 30°C for 20 min. Lanes 1 and 4, 2.8 pmol; lanes 2 and 5, 5.5 pmol; lanes 3 and 6, 11 pmol of p50 was added. The positions of ss- and duplex-containing RNAs are indicated. B, $^{32}$P-labeled 164-mer heat-denatured DNA (35 fmol) was incubated with increasing amounts of either nonphosphorylated (lanes 1–3) or phosphorylated (lanes 4–6) p50 at 30°C for 20 min. Lanes 1 and 4, 5.5 pmol; lanes 2 and 5, 11 pmol; lanes 3 and 6, 22 pmol of p50 was added. The positions of the heat-denatured and renatured DNA are indicated.

The striking finding that p50 displays both RNA annealing and melting activities in a dose-dependent manner can be of physiological significance. As it was shown earlier, p50 causes opposite effects on mRNA translatability depending on the p50/mRNA ratio (see the Introduction). According to our new findings, this effect could be explained by different conformational states of mRNA within mRNP determined by the amount of p50 bound.

p50 is a major and universal component of cytoplasmic mRNPs; therefore, it may play a key role in the mRNA spatial organization and general regulation of translation through structural adjustments of mRNAs. In this connection, it would be of interest to analyze in more detail whether the amount of mRNA-associated p50 correlates with translational regulation during stresses and during the cell cycle. It is currently known that the amount of Y-box proteins increases significantly in cancer cells (35, 36), and the amount of their mRNAs increases manyfold during liver regeneration and cell growth stimulation with serum or interleukins (37–39). The stresses (drugs, UV) result in a redistribution of Y-box proteins between the nucleus and the cytoplasm with an increase of their amount in the nucleus and a decrease in the cytoplasm (40, 41).

p50 shares functional properties with the major proteins of heterogeneous nuclear RNPs (hnRNPs), hnRNP A1, C1, and U, all of which exhibit RNA annealing activity (26, 29). Although there is no apparent sequence homology between these proteins and p50, they possess similar modular organizations comprising related RNA-binding domains with RNP 1/RNP 2 recognition motifs and auxiliary arginine/glycine-rich C-terminal domains (15, 42, 43). hnRNPs proteins as well as p50 are able to form large protein particles and arrange RNA on their surfaces (44). For hnRNP A1 it was shown that the RNA-binding domains display RNA melting activity (45, 46). Most probably, the cold shock domain of p50 is responsible for the RNA melting activity, because the major cold shock protein of E. coli (Csp A), which exhibits 43% identity to p50 cold shock domain, displays the same activity (12). Also, Y-box proteins were found within hnRNPs (7), and their involvement in processing of pre-mRNA was demonstrated (47). Thus, all of these functionally related proteins accompany mRNA at all stages of its biogenesis and seem to contribute to the appropriate packaging of mRNA in the nucleus and the cytoplasm.

The ability of p50 to accelerate the renaturation of DNA complementary strands (Fig. 3) is of a considerable interest. Because Y-box proteins exhibit broad specificity in binding to single-stranded DNA sequences (38, 48, 49), we used a plasmid polylinker DNA for our study. Strikingly, p50 shortens the half-time of DNA-renaturation from 120 h to 5 min. Assuming that p50 operates also as a transcription regulator, it is likely that its interaction with different promoter elements induces significant rearrangements of DNA structure, thereby determining the transcription efficiency (50). In addition, the DNA annealing activity may be important for DNA repair and/or recombination (51–54). Indeed, increasing evidence indicates that p50 (YB-1) is involved in DNA repair as well as in cell adaptation to therapeutic agents and UV irradiation (35, 40, 48). Of interest is our finding that the DNA annealing activity of p50 can be specifically regulated by casein kinase II phosphorylation (Fig. 6).

Although the detailed mechanism of annealing remains to be elucidated, it is obvious that p50 and functionally similar proteins accelerate RNA/DNA folding and formation of more stable duplexes (extended and containing less mismatches). The relatively high p50/RNA ratios required for annealing suggest that p50 works in a stoichiometric rather than a catalytic manner. A similar conclusion has been drawn for other proteins displaying annealing activity (55, 56). It was proposed that these proteins induce melting of the interfering secondary structure, thereby enhancing correct thermodynamically driven intermolecular base-pairing (29, 57). In addition, because of protein-protein interactions, the complementary strands of nucleic acids can be brought in close proximity,
thereby accelerating the initial rate-limiting step of the annealing reaction (29). Actually, many proteins displaying annealing activity exhibit a melting activity as well (45, 58, 59). In addition, they contain clusters of positively charged amino acid residues in their auxiliary domains, which seem to be important for annealing. The replacement or removal of only a few arginine residues from these clusters caused a drastic decrease in the annealing activities as reported for the splicing factor U2AF65 (60), nucleocapsid protein NCp7 from HIV-1 (61, 62), and NCp10 of Moloney murine leukemia virus (63, 64). These positively charged clusters are believed to be important for shielding negative charges of sugar-phosphate backbones of nucleic acid strands during annealing. The domains responsible for the annealing and melting activities of p50 are still to be determined.

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