The TATA Element and Its Context Affect the Cooperative Interaction of TATA-binding Protein with the TFIIIB-related Factor, TFIIIB*70

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We have conducted a quantitative thermodynamic study of the effects of the TATA element and TATA-flanking sequences on the assembly of complexes containing TATA-binding protein (TBP) and the TFIIIB-related factor, TFIIIB*70. TBP binds to the sequence TATAAAG in the context of the yeast U6 gene (yU6 hybrid TATA) or the adenovirus major late promoter (AdMLP) with different affinities demonstrating that the sequence context of a TATA element contributes to TBP binding. We also determined the cooperative free energies of formation of TBP-TFIIIB*70-DNA complexes on the yU6 TATA element, the yU6 hybrid TATA element and a nonconsensus TATA element. The yU6 hybrid TATA displayed a moderate, less than 5-fold, increase in TBP affinity similar to the 3-fold increase observed for the AdMLP. In contrast, the nonconsensus and yU6 TATAs increased the affinity of TBP for DNA 12- and 17-fold, respectively. Since the TBP-TFIIIB*70 cooperativity is greater on lower affinity TATA boxes and most polymerase III genes contain low affinity “TATA boxes,” we conclude that the cooperative binding of TFIIIB*70 and TBP to DNA represents an important driving force in the assembly of polymerase III-specific transcription complexes. An effect of the sequences surrounding the TATA box was also observed on TBP-TFIIIB*70 cooperativity. The mechanistic implications of the thermodynamic linkage between DNA sequence and binding cooperativity are discussed.

The TATA-binding protein (TBP)1 is required for transcription by all three nuclear RNA polymerases (pols I, II, and III) (1). This universal role of TBP is achieved, in most organisms, through its sequestration into polymerase-specific complexes (e.g. SL1, TFIID, and TFIIIB). Although sequence-specific binding of TBP to DNA is observed in two of these complexes (TFIID and TFIIIB), the efficient recruitment of each complex to the appropriate promoters in vivo is dependent upon additional interactions with other proteins termed “activating factors,” “coactivators,” and/or “initiators” (2–6). The recruitment of SL1, TFIID, and TFIIIB to DNA has been studied extensively because of the fundamental importance of these steps in transcription by the respective polymerase and because of their regulatory significance. DNA binding by TBP or its complexes appears to be a rate-limiting step for transcription initiation at many promoters (7–9). Accordingly, many regulatory factors have been described that interact directly with TBP or its associated components (4, 5).

The interaction of TBP with the TATA element has been the subject of extensive genetic, biochemical and biophysical studies. These studies have shown that TBP binds to a wide variety of sequences and that it exhibits the highest affinities for sequences of the general form TATAa/tAa/t (10). The crystal structures that have been solved of Arabidopsis thaliana TBP2 and the conserved C-terminal core of Saccharomyces cerevisiae and Homo sapiens TBP complexed with DNA containing different TATA boxes are strikingly similar and revealed a remarkable protein-DNA interaction and distortion of the DNA (11–15). TBP contacts the minor groove of DNA through a concave antiparallel β sheet that forms the underside of its “saddle-like” structure; extensive minor groove interactions are possible because the DNA is unwound, bent toward the major groove and kinked at the first and last base steps of the TATA box. Comparison of the structure of these complexes with the structures of the free A. thaliana TBP2 and C-terminal core of S. cerevisiae TBP (11, 13, 14) reveals no appreciable tertiary change but small, distinct quaternary rearrangements in the conserved C-terminal domains of the proteins upon DNA binding. The roles played by these macromolecular conformational changes in TATA element recognition and the subsequent assembly of RNA polymerase-specific transcription factors are key unanswered questions.

Although the specificity of TBP for TATA element variants has been extensively investigated, there has not been to our knowledge a thermodynamic analysis of (i) TBP binding to the same TATA box in different sequence contexts or (ii) the effects of polymerase-specific factors on TBP binding to different TATA boxes. In this report we present a quantitative thermodynamic analysis of TBP binding to the TATA element of the pol III-transcribed yeast U6 gene. We compare the binding of TBP to U6 templates containing either the wild-type TATA box or the adenovirus major late TATA box, to the adenovirus major late promoter (AdMLP) and a nonconsensus TATA element. Our results show an effect of both the TATA sequence and the sequence context on TBP’s affinity for DNA. In addition, we have examined the binding of TBP to the same four templates in the presence of the TFIIIB-related, pol III-specific transcription factor TFIIIB*70. Effects of the TATA sequence and its context were also evident in the assembly of the TBP-TFIIIB*70-DNA complex. This work together with other studies provides insights into the role of DNA structure in TBP binding and the assembly of polymerase-specific complexes.

* This work was supported in part by National Institutes of Health Grants GM55155 to (M. B.) and GM42728 (to I. M. W.) and by grants from the Hirschl/Weill Caulier Trust (to I. M. W. and M. B.). The costs of publication of this article were defrayed in part by the payment of page charges. This article must therefore be hereby marked “advertisement” in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.
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1 The abbreviations used are: TBP, TATA-binding protein; AdMLP, adenovirus major late promoter;
EXPERIMENTAL PROCEDURES

Protein Preparations—Recombinant S. cerevisiae TBP and TFIIIB<sub>70</sub>, were prepared, quantitated, and stored as described previously (16–18). A single preparation of TBP and TFIIIB<sub>70</sub> was used for all experiments.

Preparation of DNA probes—Plasmid pM4 (yU6 TATA), contains the sequence from −119 to +73 relative to transcription start site of the yeast SNR6 gene and was constructed by cloning a Cal-EcoN1 restriction fragment from p544-H6 (a gift from Dr. D. Brow) into BamHI-ClaI digested pBlPF72 following Klenow fill-in of the EcoN1 and BamHI ends. Plasmid pM5 (yU6 hybrid TATA) is identical to pM4 except for two nucleotide substitutions (TATAAATA to TATAAAAG) which change the sequence of the TATA element to that found in the upstream promoter region of SNR6, a pol III-transcribed gene encoding U6 snRNA; (ii) yU6 hybrid TATA, which is identical to yU6 TATA except for two nucleotide substitutions (TATAAATA to TATAAAAG) which change the sequence of the TATA element to that found in the AdMLP; and (iii) a construct containing the nonconsensus TATA element, TATAGGTG. The binding of TBP to the yU6 TATA, which contains the upstream promoter region of SNR6, a pol III-transcribed gene encoding U6 snRNA; (ii) yU6 hybrid TATA, which is identical to yU6 TATA except for two nucleotide substitutions (TATAAATA to TATAAAAG) which change the sequence of the TATA element to that found in the AdMLP; and (iii) a construct containing the nonconsensus TATA element, TATAGGTG. The binding of TBP to the yU6 TATA, the yU6 hybrid TATA and the nonconsensus TATA results in clear and specific protection under the experimental conditions used in these studies (Fig. 1, panels A and C and data not shown); nonspecific binding of TBP is not observed over the range of TBP concentrations investigated. Equilibrium titration of these substrates with TBP are well described by the Langmuir binding polynomial, as was observed previously for the AdMLP and E4 TATA elements (16, 17). The TBP binding isotherms determined for each of these substrates are shown in Table I. The order of affinity of the TATA elements for TBP is TATAAAAG > TATAAATA > TATAGGTG. Interestingly, the context of the TATA element has a small but significant effect on TBP binding. The affinity of TBP for the yU6 hybrid TATA is 0.3 kcal/mol less negative than the previously reported TBP affinity for the AdMLP (Table I); this difference is statistically significant due to the high precision of the binding isotherms. Thus, the sequences surrounding the TATA box modulate TBP binding.

RESULTS

TBP and TFIIIB<sub>70</sub> display a moderate 3-fold cooperativity in their assembly onto the TATA element of the AdMLP (17). In the present study, the effect of the TATA sequence and its context on TBP-TFIIIB<sub>70</sub> DNA binding cooperativity has been explored. Three substrates were employed in this analysis: (i) yU6 TATA, which contains the upstream promoter region of SNR6, a pol III-transcribed gene encoding U6 snRNA; (ii) yU6 hybrid TATA, which is identical to yU6 TATA except for two nucleotide substitutions (TATAAATA to TATAAAAG) which change the sequence of the TATA element to that found in the AdMLP; and (iii) a construct containing the nonconsensus TATA element, TATAGGTG. The binding of TBP to the yU6 TATA, the yU6 hybrid TATA and the nonconsensus TATA results in clear and specific protection under the experimental conditions used in these studies (Fig. 1, panels A and C and data not shown); nonspecific binding of TBP is not observed over the range of TBP concentrations investigated. Equilibrium titration of these substrates with TBP are well described by the Langmuir binding polynomial, as was observed previously for the AdMLP and E4 TATA elements (16, 17). The TBP binding isotherms determined for each of these substrates are shown in Table I. The order of affinity of the TATA elements for TBP is TATAAAAG > TATAAATA > TATAGGTG. Interestingly, the context of the TATA element has a small but significant effect on TBP binding. The affinity of TBP for the yU6 hybrid TATA is 0.3 kcal/mol less negative than the previously reported TBP affinity for the AdMLP (Table I); this difference is statistically significant due to the high precision of the binding isotherms. Thus, the sequences surrounding the TATA box modulate TBP binding.
To determine whether the TBP-TFIIIB70 DNA binding cooperativity is linked to the sequence of the substrate DNA, TBP titrations were conducted in the presence of constant concentrations of TFIIIB70 on the yU6 TATA, the yU6 hybrid TATA and the nonconsensus TATA, as previously conducted with the AdMLP (17). As observed with the AdMLP, TFIIIB70 alone does not detectably bind to these DNA molecules (data not shown). However, unlike the AdMLP, the DNAase I footprints observed on the yU6 and yU6 hybrid promoters show sites of DNAase I protection within the complete TATA element. The isotherms, represented as "solid curves," result from fitting the data to the Langmuir expression for single site binding, \( Y_{\text{BP}} = \frac{K_{\text{d}}^{n}[\text{TBP}]^{n}}{1 + K_{\text{d}}^{n}[\text{TBP}]^{n}} \) where \( n = 1 \).

Densiometric scans in the direction of electrophoresis across the yU6 TATA element are shown in Fig. 3 and define the footprint borders of the TBP-DNA and TFIIIB70-DNA complexes. As can be seen in Fig. 3A, the TBP footprint on the yU6 TATA extends from \(-35\) to \(-20\) (15 base pairs), similar to the TBP footprint reported previously on this gene (23). In addition, slight protection around \(-50\) was observed. Analysis of TFIIIB7 in the yU6 TATA complex (Fig. 3B) revealed protection from \(-35\) to \(-20\) and from \(-13\) to \(+4\) with a greater degree of protection around \(-50\). A comparable region of DNAase I protection at \(-50\) within the complete TFIIIB7-yU6 TATA complex was reported by Joazeiro et al. (23). TFIIIB7-yU6-specific interactions upstream and downstream of the yU6 TATA box are consistent with these findings. The region between \(-20\) and \(-13\) is poorly cut by DNase I, therefore protein protection could not be evaluated for these base pairs.

Since TFIIIB7 binding in the absence of TBP was not observed under the conditions employed, the cooperativity between TBP and TFIIIB7 was analyzed by determining the effect of increasing concentrations of TFIIIB7 upon the TBP binding isotherm. In the presence of TFIIIB7, protection of the TATA element commenced at lower TBP concentrations compared with the TBP titration alone for each DNA tested (Fig. 1; data not shown). This effect is clearly reflected in the binding isotherms; TFIIIB7 shifts the TBP binding isotherms to lower concentrations for each DNA substrate assayed (Fig. 2B, data not shown). The increase in the observed affinity of TBP for these TATA sequences reveals the positive cooperative interaction between the two proteins. The intrinsic cooperativity for the simultaneous binding of the two proteins to each of the DNA substrates, \( \Delta G^{\circ}_{\text{TBP/TFIIIB70}} \), is determined at the plateau where \( \Delta G^{\circ} \) becomes independent of [TFIIIB70]; at this point, all of the binding cooperativity between the two proteins is partitioned into the TBP isotherms (see "Experimental Procedures").

For the yU6 TATA, the yU6 hybrid TATA and nonconsensus TATA probes, the results of these experiments are shown in Fig. 4 as the energy difference (\( \Delta G^{\circ} \)) referenced to the "TBP alone" titrations. The values of \( \Delta G^{\circ}_{\text{TBP/TFIIIB70}} \) determined for each of the substrates are summarized in Table I. A clear result is that \( \Delta G^{\circ}_{\text{TBP/TFIIIB70}} \) is 1.0 kcal/mol more negative for the yU6 promoter compared with the AdMLP. The TBP-TFIIIB70 DNA binding cooperativity for the nonconsensus TATA is only slightly less than that of yU6. Thus, at 30 °C, the temperature of these assays, the TBP-TFIIIB70 cooperativity increases the affinity of TBP binding to the nonconsensus and yU6 TATAs 12-fold and 17-fold, respectively. Remarkably, much more moderate TBP-TFIIIB70 DNA binding cooperativity is observed on the yU6 hybrid TATA, which contains the AdMLP TATA element in the yU6 context (Table I). Interestingly, while the yU6 hybrid and the AdMLP promoters contain the same TATA sequence, the \( \Delta G^{\circ}_{\text{TBP/TFIIIB70}} \) for the yU6 hybrid promoter remains more negative than that of the AdMLP. Thus, the data demonstrate that both the sequence of the TATA element and its context contribute to the magnitude of the TBP-TFIIIB70 cooperativity.

DISCUSSION

The DNA sequence of the TATA element is a major determinant of the affinity of TBP for a DNA substrate (10, 24, 25). The relative TBP affinities from the present analysis are AdMLP (TATAAAAG) > yU6 hybrid TATA (TATAAAAG) > yU6 TATA (TATAAAATA) > nonconsensus TATA (TATAGGTTG) (Table I). This order of TATA element affinities is consistent with a broader analysis of TATA elements being conducted under identical experimental conditions; these data indicate that there is a 1.0–1.5 kcal/mol “penalty” associated with a variety of deviations from the consensus sequence when at least one consensus “half-site” is maintained. Thus, the global conformation of the TBP-nonconsensus DNA complex is likely to be comparable to the other complexes studied.

The AdMLP and yU6 hybrid TATA contain the same TATA element in a different sequence context. The thermodynamics of TBP binding to these substrates provides direct evidence for a small but statistically significant context effect on TATA element binding by TBP (Table I). Our direct measurements of TBP binding are consistent with the results of an in vitro selection study that found clear preferences for the flanking base pairs among 35 TATAAAAG sequences selected for high affinity TBP binding (10). The preferred bases at positions -4,
−3, −2, −1, and +9 were A/G, G, A/G, G/C and G/C, respectively. The natural context of the AdMLP is a perfect match at these positions. Correspondingly, a bias against specific bases was observed at the above positions as well as at position +10. Three of these unfavored bases (T at −3, A at +9, and T at +10) are found in the normal context of the U6 TATA box. Thus, the difference in the affinity of TBP for the AdMLP and the yU6 hybrid TATA is in agreement with the previously proposed optimal TATA-flanking sequences.

TATA element binding by TBP is characterized by slow association and dissociation kinetics. The association of S. cerevisiae TBP for TATA elements proceeds at rates significantly slower than diffusion-limited following simple second-order kinetics over several orders of magnitude of TBP concentration (16, 18, 26, 27, 3). Stopped-flow fluorescence resonance energy transfer (FRET) studies have demonstrated that the binding of TBP and the bending of the DNA occurs simultaneously at

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V. Petri, M. Hsieh, E. Jamison, and M. Brenowitz, unpublished data.
TBP/TFIIIB70, for the yU6 TATA, yU6 hybrid TATA, and nonconsensus TATA (C). The energy differences, \( \Delta G^{\text{yU6 hybrid TATA}}_\text{TATA} \) for the yU6 TATA, yU6 hybrid TATA, and nonconsensus TATA are referenced to the corresponding TBP alone titrations (Fig. A).

Since no contacts outside the 8 base pair TATA element have been observed in either structural or biochemical studies of TBP-DNA interactions, the effect of sequence context on TBP binding could possibly be indirect. For the few cases where it has been investigated, base pair substitutions within a TATA box reduce TBP binding affinity through an increase in the complex dissociation rate (25). In contrast, the difference in TBP binding affinity between the AdMLP and yU6 hybrid promoters (Table I) is manifest in the rate of association of TBP with the DNA. Thus, the observed context effect may be due to differences in the conformational distributions of the promoters, biasing the distribution either toward or away from conformations capable of forming a productive encounter complex with TBP. Increased DNA flexibility would broaden the conformational distribution and hence might decrease the rate of association. Alternatively, structurally constrained regions of DNA (such as the runs of poly(A) that flank the yU6 TATA element) might bias the conformational distribution unfavorably (10).

Numerous TATA elements have been shown to direct the assembly of Pol II- and Pol III-specific complexes under a variety of experimental conditions (for example see Refs. 24, 28, and 29). To further investigate the mechanisms by which transcription preinitiation complexes form, the interaction of TBP and TFIIIB70 on different TATA elements and on the same TATA element in different contexts was quantitatively characterized. The binding of TFIIIB70 to DNA in the absence of TBP was not detectable in the DNase I footprinting assay, therefore the cooperativity between TBP and TFIIIB70 was quantitated by monitoring the effect of TFIIIB70 concentration on the TBP-promoter binding isotherms. Interestingly, the two lower affinity TATA elements (yU6 and nonconsensus, Table I) displayed substantially higher cooperativity than the higher affinity TATA elements (AdMLP and yU6 hybrid). This observation suggests that the TBP-TFIIIB70 cooperativity plays a more important role in the assembly of Pol III transcription complexes than was apparent from our previous study using the AdMLP (17). With a few notable exceptions (e.g. metazoan type III genes and the yeast U6 gene (1)), Pol III genes are generally thought to be TATA-less. However, a recent analysis of the sequences upstream of tRNA genes in several organisms indicates that, in the majority of cases, TATA-like sequences are found 30–35 base pairs 5’ to the putative transcription start site (30). Thus, while the mechanism of the TATA element-mediated enhancement of TBP-TFIIIB70 cooperativity is not yet clear, our findings show that an important role for TFIIIB70 involves its ability to drive preinitiation complex assembly by increasing significantly the affinity of the TBP-TFIIIB70 complex for DNA. Similar cooperativity has been observed for the formation of the TBP-TFIIIB-DNA complex (31, 32).

In addition to the dependence of the TBP-TFIIIB70 cooperativity upon the sequence of the TATA element, the cooperativity is also dependent on the sequence context surrounding the TATA box. We reproducibly observed that the magnitude of the cooperativity on the U6 hybrid TATA was higher than on the AdMLP (Table I). Whereas the sequences flanking the TATA element in the AdMLP are optimal for TBP binding, the TATA element context cooperativity on the U6 hybrid TATA was higher than on the yU6 TATA element, indicating that the sequence context of the TATA element is important for TBP binding.

30 °C, with no evidence of a diffusion-limited intermediate in the reaction pathway (18). The available data support a kinetic mechanism in which TBP binding is limited by the probability that TBP-DNA “encounter complexes” overcome a high activation energy barrier and proceed down the reaction pathway (18). It was hypothesized that TBP samples the population of DNA conformations in solution and productively binds to only a small fraction of these (18).

4 TBP oligomerization plays no role in DNA binding under the experimental conditions of these studies (37).

5 A. K. M. Mollah, M. Librizzi, I. Willis, and M. Brenowitz, unpublished data.

**FIG. 4.** Comparison of free energy differences for TBP binding to the yU6 TATA, yU6 hybrid TATA, and nonconsensus TATA. A series of DNase I footprint titrations were conducted at a series of constant TFIIIB70 concentrations on the yU6 TATA (A), yU6 hybrid TATA (B), and nonconsensus TATA (C). The energy differences, \( \Delta G^{\text{yU6 hybrid TATA}}_\text{TATA} \) for the yU6 TATA, yU6 hybrid TATA, and nonconsensus TATA are referenced to the corresponding TBP alone titrations (Fig. 2, A and B, data not shown) and are a measure of cooperativity. Only at the energy difference plateau does the fractional saturation by TBP become independent of TFIIIB70 concentration and \( \Delta G^{\text{yU6 hybrid TATA}}_\text{TATA} = \Delta G^{\text{yU6 hybrid TATA}}_\text{TFIIIB70} \), the cooperative free energy between TBP and TFIIIB70 (see “Experimental Procedures”). Since a limited number of experiments were performed to establish the energy difference plateau for the yU6 hybrid TATA, the transition curve is less reliable at low TFIIIB70 concentrations than the curves in panels A and C.
Several mechanistic interpretations are consistent with the observed TATA element and flanking sequence effects on TBP-TFIIB70 cooperativity. TFIIB70 may make a specific contact(s) with a base(s) within the TATA element. Comparison of the AdMLP, yU6, and nonconsensus sequences shows that all three possess a TATA consensus half-site. The only other base that the yU6 and nonconsensus sequences have in common is a thymine in the 7th position substituting for adenine in the AdMLP (Table I). Substitution of just this base in the AdMLP, yU6, and nonconsensus sequences shows that subtle structural changes within a TATA element can have large energetic effects. This nucleotide substitution is isosteric with regard to the presentation of hydrogen bond donors and acceptors in the minor groove to which TBP binds. However, an alternate hydrogen bond donor and acceptor pattern is presented in the major groove of the TATA element. At saturating concentrations of TBP and TFIIB70 we have observed additional DNase I protection of bases within the AdMLP TATA element in comparison to the protection provided by TBP alone (17). This suggested that TFIIB70 is positioned on the underside of the TBP-induced DNA bend. Therefore it is possible that TFIIB70 may interact with the T7 base pair in the major groove. For this hypothetical interaction to affect TBP-TFIIB70 cooperativity and not merely the intrinsic binding of TFIIB70, the interaction must indirectly affect TBP binding. Since the second DNA kink in TBP-DNA complexes is between positions 7 and 8, TFIIB70 may stabilize the kinked conformation and thus facilitate TBP binding.

An alternative mechanism is that TFIIB70 interactions with TBP differentially affect the ability of TBP to form the specific ensemble of interactions present in TATA elements with T-A versus A-G base steps at the 3' kink. This possibility is appealing since genetic studies have implicated the amino-terminal H2 helix of TBP, which sits directly above the critical phenylalanine residues of TBP as a binding site for TFIIB70 (33). The fact that the relative orientation of the two subdomains of TBP changes upon TATA element binding (free versus co-crystal structures) suggests that TBP conformational changes may play a role in the cooperative binding of TBP with other transcription factors.

Sequence-specific interactions between TFIIB70 and the flanking DNA could also play a role. Examination of the eukaryotic TFIIB-TBP-DNA co-crystal structure and the homologous archaeal TFB-TBP-DNA co-crystal structure in light of the extensive sequence homology between TFIIB70-TFIIB and TFB predicts interactions between TFIIB70 and sequences adjacent to the TATA box (34, 35). In support of this possibility, a recent study has uncovered a sequence-specific interaction between human TFIIB and a guanosine at position –3 relative to the TATA box. In addition, a cryptic nonspecific DNA binding domain has been uncovered recently in the carboxyl-terminal 86 residues of TFIIB70 (36); this domain of TFIIB70 is likely to contribute to complex stability. Protection of bases outside of the TATA box in the TBP-TFIIB70 complex on the yU6 promoter represents further evidence that TFIIB70-DNA interactions play a role in stabilizing the ternary complex (Fig. 3). Studies to examine each of these possible mechanisms are in progress.

Acknowledgment—We thank Elizabeth Jamison for providing recombinant TBP.

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The TATA Element and Its Context Affect the Cooperative Interaction of TATA-binding Protein with the TFIIB-related Factor, TFIIB

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J. Biol. Chem. 1998, 273:4563-4568.
doi: 10.1074/jbc.273.8.4563

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