Permanganate probing has been used to follow the progress and ATP dependence of promoter opening during activated adenovirus E4 initiation and clearance. Using templates designed to restrict synthesis to defined positions, formation of a 3-nucleotide-long RNA was found to be sufficient to trigger expansion of the initial transcription bubble. This occurred by a discrete transition that expanded the downstream limit of melting from position 1 to 15. Subsequent clearance of the bubble from the promoter region also occurred without detectable intermediates. Thus, initial opening, extension, and the clearance of the promoter bubble appear to occur as discrete, unique transitions. The apparent $K_m$ values for these three steps were determined to be near 5, 9, and 50 $\mu$M, respectively. Comparison of these values with ATPase activities within known transcription factors raises the possibility that different activities could be responsible for each step.

Transcription initiation by RNA polymerase II can be divided into a number of steps (reviewed in Ref. 1). Initially, the polymerase is recruited to the promoter in the closed complex state. In this state, the DNA remains fully double-stranded. Transcription cannot initiate because the template strand cannot be read in double stranded form. In a series of post-recruitment steps, the DNA is opened over the transcription start site, allowing initiation to begin. During the subsequent promoter clearance steps, the polymerase elongates away from the promoter along with the transcription bubble of melted DNA (2). Each round of initiation requires that a new polymerase be recruited into closed complexes and that the DNA be reopened.

Transcription initiation has long been known to require hydrolysis of the $\beta$-$\gamma$ bond of ATP (3, 4). The hydrolysis was shown to be in a postrecruitment step that preceded elongation (5). Subsequently, permanganate probing was used to identify open complexes, and ATP was shown to be required to open the DNA within closed complexes at a variety of promoters (6, 7). Promoter clearance was also shown to depend on ATP (2, 8, 9).

More recently the postrecruitment pathway has been subdivided into several steps. Parallel studies in two different systems identified three consecutive postrecruitment steps (10, 11). In the first step, the DNA upstream from the start site is opened (to form the preinitiation open complex (POC)). In the second step, the melted bubble is enlarged as DNA downstream from the start site is opened (to form the initiation open complex (IOC)). Formation of the IOC is triggered after initiation of RNA synthesis. When ATP is depleted, the POC decays rapidly, but the IOC does not, implying that the IOC has much higher stability. Finally, the polymerase and the bubble exit the promoter region as the complex enters elongation mode. In at least one of these systems, ATP hydrolysis is required for all of these postrecruitment steps and also for the formation of the first bond of the RNA (11).

Because each of these steps has the potential to be regulated, some effort has been applied to identify the activities that catalyze them. General transcription factors TFIID and TFIIH have been implicated in these postrecruitment steps (8, 12). Mutations that inhibit a helicase activity of TFIIH impair the ability to reach the IOC stage (13). Several lines of evidence implicate the C-terminal domain kinase activity of TFIIH in the final conversion to the elongation stage (2, 14–16). Both helicase and kinase activities use ATP, which supports their involvement in transcription initiation.

Several important issues surrounding these postrecruitment steps remain to be resolved. These issues center on how the promoter is opened initially to form the POC and how the POC is converted to the IOC during initial RNA synthesis. We showed previously that all postrecruitment steps require ATP hydrolysis (11). This includes the initial opening of the DNA and the formation of the first RNA bond. There have not been studies to identify which activities use ATP in these steps. Although the TFIIH helicase is an obvious candidate activity for steps prior to the IOC stage, it has not been implicated specifically in POC formation. Moreover, helicases rarely if ever initiate opening from unmodified fully double-stranded DNA without assistance from other activities (17). Thus, this activity is likely required to extend the initial bubble, but what causes the initial bubble to form is not known.

In addition, the POC to IOC conversion appeared to occur differently in the two systems studied. In one case, the conversion occurred in a discrete step triggered by the initiation of RNA synthesis (11). In the other case the conversion was gradual and was not complete until a substantial length of RNA had been produced (10). The more rapid and discrete stabilization process was observed in an activated unfractionated system, allowing for the possible involvement of factors absent from highly purified basal system. Thus, it is not yet clear how many activities are involved in forming and clearing the open DNA during initiation. Significant uncertainty surrounds how DNA opening is initiated and how RNA synthesis is involved in extending and stabilizing the open complex.

This study focuses on how ATP is used in order to define how many activities might be involved in these processes. In addition, it explores the applicability of the discrete model for conversion to the IOC using an experimental system with tighter regulation of RNA synthesis than used previously (11).
The results lend further support for the postulated pathway for formation of the IOC and also provide constraints on the types of activities that may be involved in the use of ATP during initiation.

**EXPERIMENTAL PROCEDURES**

**General Materials**—Ultrapure NTPs, dNTPs, and 3-O-methyl-GTP were from Amersham Pharmacia Biotech. Ribonucleotide UpA and ATP·S were from Sigma. The DNA template G9E4T contains nine Gal4 binding sites upstream of a truncated adenovirus E4 promoter (18).

Potassium Permanganate Footprinting—Permanganate probing in a HeLa extract was done as described (6, 11). To measure the $K_m$ for the POC formation, various concentrations of dATP were added 2 min before permanganate treatment. To measure the $K_m$ for the IOC formation, 2 mM UpA and 25 μM CTP were added before the dATP and permanganate treatment. To measure the $K_m$ for the promoter clearance, various concentration of dATP were added for 2 min, followed by the addition of the elongation mixture (50 μM GTP, CTP, UTP, and 2.5 μM ATP) for 2 min and permanganate treatment.

Quantitation of results used ImageQuant software for PhosphorImager results (Molecular Dynamics, Inc., Sunnyvale, CA). Background subtraction used a common region of each lane, not associated with melting. Signals were normalized to the strongest POC or IOC signal or the maximum amount of clearance in appropriate experiments. Data from several experiments were averaged and fit into the classic Michaelis-Menten equation using SigmaPlot (version 4.0, SPSS Inc.). The $K_m$ values and S.D. values were calculated using the same software.

**RESULTS**

Full Bubble Extension Is Complete when a 3-Nucleotide-long RNA Is Made—The first experiments address the role of initial RNA synthesis in extending the POC bubble to form the stable IOC. In our prior study of the activated adenovirus E4 promoter, this transition was sudden and discrete (11); i.e., when formation of a 3-mer RNA was triggered by the addition of dinucleotide UpA and CTP, the downstream edge of the transcription bubble moved from near position 1 to near position 15. This result contradicted with results from a basal adenovirus major late system, where the downstream edge extended gradually as the initial bonds of the RNA were made (10). Another difference was that only the latter study used a series of constructs that stop synthesis definitively at set points by incorporating the chain terminator 3'-O-methyl-GTP. By including G at different template locations, one can use such templates to eliminate potential nucleotide misincorporations (10). We created a series of modified templates to test the discrete model in the situation where chains can be terminated definitively with 3'-O-methyl-GTP.

The parent G9E4T template contains nine Gal4 binding sites upstream of an adenovirus E4 promoter. Transcription starts within the T9A region approximately 25 base pairs downstream from the TATA box. For convenience, we designate the last thymidine in the T6 sequence as +1. Fig. 1A shows the series of templates constructed and used in these studies. Each variant has a G substituted in a different position, including positions 2, 3, 4, and 5. As discussed elsewhere, the use of 3'-O-methyl-GTP allows synthesis to be restricted to RNAs terminated at these positions (10). We confirmed that each of these templates can be transcribed (data not shown).

The transition through the different stages of open complex formation can be visualized using permanganate footprinting (6). Permanganate can selectively modify the thymidine residues in the single strand region of the DNA template, thus causing a stop when copied with Taq polymerase in a subsequent primer extension protocol. The region that has been melted is detected as a series of hypersensitive bands upon autoradiography of the primer extension products separated on gels. In this set of experiments, permanganate is used to detect the downstream limits of bubble formation on templates where G nucleotides are present to ensure termination at different points.

The experiment of Fig. 1B begins by showing the bubble upstream from the start site that is triggered by the addition of dATP to closed transcription complexes (lane 2 versus lane 1). Lane 3 shows the extension of the bubble to far downstream positions when ATP and CTP are added to closed complexes on the original template with initial sequence TACAC. These controls show the limits of permanganate-sensitive regions for the POC (lane 2) and the IOC (lane 3).

In the next experiment, the DNA with the initial sequence TAGAC was used to restrict synthesis in conjunction with the chain terminator 3-O-methyl-GTP. Lane 5 shows the permanganate signal obtained when this template is used with the dinucleotide UpA and 3'-O-methyl-GTP (expected product of UpApG). The addition of these nucleotides has triggered the IOC pattern (compare with lane 3) rather than the POC pattern (compare with lane 2). The overall signal is somewhat weaker, perhaps indicating that the conversion is not quite complete. The downstream edge of the bubble appears to have reached its full extension, previously shown to approach position 15.

Although the presumptive UpApG product in this experiment contains two RNA bonds, only a single one has formed due to the use of a dinucleotide primer. Another experiment indicates that the existence of an RNA product of 3 nucleotides in length may be more important than the synthesis of a single bond. When ATP and 3'-O-methyl-GTP are used with this same
template (lane 4) there is, at best, only weak extension of the bubble to form the IOC. Under these circumstances the expected product is only a 2-mer, pppApG. The comparison indicates that formation of a 3-nucleotide-long RNA is sufficient for formation of an IOC with the bubble extended fully to near position 15.

This discrete transition is also observed in protocols allowing extension to positions 4 and 5 without dinucleotide primers (lanes 6 and 7). These used ATP, CTP, and 3′-O-methyl-GTP on templates TACAG (potential product pppApCpApG) and TACACG (potential product pppApCpApGp). The patterns in lanes 6 and 7 are slightly more hypersensitive in the downstream region (compare with lane 5), indicating a slightly higher efficiency of IOC formation. The downstream limit of the extended bubble appears to be the same in all three circumstances.

It should be emphasized that these experiments use a high concentration of 3′-O-methyl-GTP, so the possibility of producing longer transcripts due to misincorporation is very low. Direct observation of RNA did not show such products (Ref. 19 and data not shown), but they would not necessarily be detectable in the crude extract system. In the system with purified factors where longer products could be seen, 3′-O-methyl-GTP was able to arrest chain elongation at the first G position (10). We further confirm the termination efficiency of 3′-O-methyl-GTP by using a TAGAG template. The combination of ATP and GTP (with the expected product pppApGpApG) is sufficient to cause IOC formation (lane 8). However, the substitution of 3′-O-methyl-GTP for GTP blocks IOC formation (lane 9), demonstrating that it has prevented any read-through due to misincorporation.

The data indicate that when the IOC forms the opening always extends as far as position 15 (lanes 3 and 5–8), whereas the POC opening never extends beyond the start site (lanes 2, 4, and 9). The results indicate that the transition from POC to IOC is not gradual and is accompanied by a sudden extension of the transcription bubble. This extension happens when an RNA as short as a 3-mer is formed and appears to be somewhat more efficient when longer RNA is made. The results contrast with a prior study in a different experimental system in which the leading edge of the bubble extended gradually as the RNA became longer (Ref. 10; discussed below).

The Apparent Km Values for POC and IOC Are in the Range of 4–10 μM—It is apparent from these and prior data that the formation of the POC and IOC are different processes. Formation of both complexes requires ATP. It is not yet known if the same activities are involved in the creation of these two complexes. Recent results using mutant forms of TFIH measured the formation of the IOC only; the effect of mutation on the POC was not assessed (see Introduction). In order to place constraints on which activities might be involved, we measured the Km for these steps. We use dATP rather than ATP to avoid potential complications from the use of ATP as an elongation substrate. The result will allow these Km values to be compared with each other and with values for various activities that are candidates for triggering formation of the POC and the IOC.

To measure the apparent Km for dATP, its concentration was varied, and the extent of POC formation was assayed. dATP concentrations up to 125 μM were added to reactions. Two minutes later, permanganate was added, and opening was assayed in the standard manner. The result (Fig. 2A) shows the increasing POC signal that is observed with increasing dATP concentration.

The extent of POC formation was quantified by PhosphorImager analysis. The average of four trials was used in the data display of Fig. 2B. The results indicate an apparent Km for dATP of about 4.8 μM with an S.D. value of 0.9 μM. This value is consistent with previous indications that the Km of POC formation should be under 10 μM for dATP (20). The apparent Km for IOC formation was determined using a protocol modified to trigger bubble extension. In this protocol, UpA and CTP are included as substrates for UpApC formation. Varying concentrations of dATP are added to trigger IOC formation. Fig. 3A shows the resulting permanganate patterns. Part of the IOC-specific signal (bar at right) was quantified and analyzed as for the IOC data. The results of five trials were averaged and are shown plotted in Fig. 3B. The apparent Km for dATP for IOC formation is about 8.5 μM, with a S.D. of 1.6 μM.

This IOC Km is approximately 2-fold higher than that obtained for POC formation. Qualitatively, the raw data in the autoradiograph also confirm that it takes less dATP to trigger the upstream opening typical of POC formation than to trigger bubble extension to form the IOC. For example, the upstream melted DNA signal in the fifth lane from the left is nearly saturated as judged by comparison with the seven lanes to its right. However, in this same lane, the IOC-specific part of the signal is significantly below saturation (see bracket at right). This comparison shows directly that bubble extension requires a higher dATP concentration than upstream opening, although the difference may be modest.

IOC and POC Formation Are Inhibited Similarly by ATPγS—It was shown previously that a large excess of the nonhydrolyzable ATPγS inhibited formation of both the POC and the IOC (11, 20), consistent with prior reported effects during the early stage of transcription initiation (5, 21). If the activities catalyzing both steps are similar, they would be expected to be affected similarly by this inhibitor. In this exper-
The experiment used a low concentration of inhibitor to compare the responses in formation of the POC and the IOC.

The assays used were like those just described but performed in the presence of 25 \( \mu M \) ATP\(_3^S\). The amount of dATP was varied from 0 to 125 \( \mu M \). Separate experiments determined the amount of POC formed (Fig. 4A) and IOC formed (Fig. 4B). The inhibition is apparent in both cases; i.e., at 12.5 \( \mu M \) dATP there is little formation of POC (Fig. 4A, lane 3) as well as little formation of IOC (Fig. 4B, lane 3). This is in contrast to the extensive formation of both complexes at 12.5 \( \mu M \) dATP seen when no inhibitor was present (see Fig. 3). Qualitatively, both complexes are inhibited similarly. Quantitative analysis (not shown) indicates that the apparent \( K_m \) for each process is raised by roughly 1 order of magnitude in the presence of 25 \( \mu M \) ATP\(_3^S\). We infer that the activities that catalyze POC and IOC respond similarly to this inhibitor.

**The Promoter Clearance Step Has an Apparent \( K_m \) Near 50 \( \mu M \)—**The step following IOC formation is the escape of RNA polymerase from the promoter into elongation phase. The escaped polymerase is accompanied by the transcription bubble, and both clear the promoter region together. We devised an assay to follow the disappearance of the bubble from the promoter region. The disappearance is monitored at different dATP concentrations to evaluate the \( K_m \) for the clearance step.

Such an assay is complicated by the need for ATP as an elongation substrate for transcription. Thus, ATP must be present to allow the polymerase to move away from the promoter. But because the steps prior to clearance also require ATP, the aggregate effects of low ATP could be confusing. This complexity can be bypassed if the \( K_m \) for clearance is substantially higher than that for the prior steps. This turned out to be the case, and the following protocol proved to be successful.

In this protocol a mixture of 50 \( \mu M \) each of CTP, GTP, and UTP and 2.5 \( \mu M \) ATP is added to reaction mixtures. This amount of ATP is sufficient to allow POC formation (Fig. 5A, leftmost lane). However, it is too low to allow efficient clearance, as indicated by the retention of the permanganate signal over the promoter region. If 1 \( \mu M \) dATP is added (rightmost lane), the permanganate signal is substantially depleted. This demonstrates that a high concentration of dATP can trigger clearance of the bubble.

The experiment is then to simply vary the concentration of dATP and follow the clearance of the bubble from the promoter region. Fig. 5A shows the resulting autoradiographs, which demonstrate progressive degrees of clearance triggered by increasing dATP concentrations. The transition to clearance is a discrete rather than a gradual process; i.e., there is no evidence in the patterns that inefficient clearance at low dATP concentrations gives complexes where the bubble has changed its location. Instead, the patterns at low and high dATP concentrations are essentially similar; there is just a lower degree of melting upstream from the start site at the high concentrations at which clearance has occurred efficiently.

The data were analyzed quantitatively by PhosphorImager analysis, and four trials were averaged (Fig. 5B). The apparent \( K_m \) for promoter clearance is 53 \( \mu M \), with a S.D. of 12 \( \mu M \). This is obviously greater than the \( K_m \) values for the prior steps, as measured above.

Overall, the data show that the three consecutive postre-
trials were used to derive the best-fit curve. The $K_m$ of elongation mix (final concentration 2 concentrations of dATP were added for 2 min, followed by the addition concentrations used are (from the 53.4 and maintained? 2) What protein factors are involved, and does questions have arisen. 1) How is the bubble extension triggered form a fully stable open complex. Two unresolved types of prior uncertainty involves the relationship between initial un-

The Activated Transcription System Involves Early and Dis-
crete Bubble Extension during Initiation—A primary area of prior suspicion involves the relationship between initial un-
stable promoter opening and the extension of the bubble to form a fully stable open complex. Two unresolved types of questions have arisen. 1) How is the bubble extension triggered and maintained? 2) What protein factors are involved, and does the same activity catalyze the initial opening and the exten-
sion? We consider the transition first.

The current data indicate that the transition is virtually complete when a 3-nucleotide-long RNA is made. The opening extends a full helix turn downstream from the edge of the RNA, and the entire downstream region appears to open at once. Thus, the transition appears to be between one discrete com-
pact and another.

Aspects of these data differ from a prior study at the aden-
virus major late promoter (10). Some of these differences were seen previously (11). In the major late case, the transition occurred gradually and apparently was not between two fully discrete complexes. Instead, as the RNA grew progressively longer the bubble also grew progressively longer. There are several differences between the two experimental systems, and the new data reported here help to decide which differences are the most relevant. One difference in the prior studies was that only the major late templates were engineered to prevent un-
intended read-through via placement of sites for the chain terminator 3'-O-methyl-GTP. In the current study, we engi-
eered an analogous series of templates at the E4 promoter. The use of these showed that this was not the source of the different results in the two systems; the more detailed studies presented here still demonstrated a discrete transition early in the initiation process. Other data indicate that the different promoter used was also unlikely to be the source of the differ-
ence; i.e., prior less detailed study of the major late promoter showed that formation of a 3-nucleotide-long RNA was suf-
cient to catalyze opening downstream the start site (12, 22).

The remaining system difference is that the current E4 sys-
tem relies on activated transcription from unfractionated ex-
tracts, whereas the comparison major late promoter study used a highly purified basal system. We suggest that factors present in the unfractionated activated system allow the transition to occur earlier and more efficiently. Thus, the activated system can trigger the discrete transition as soon as a very short RNA is made. We suggest that the normal pathway is likely to proceed in this manner.

Potential Activities Used in the Three-step Postrecruitment Pathway—The current data show that the three postrecruit-
ment steps have a progressively higher $K_m$ for dATP. The transcription machinery has multiple ATPase activities within factor TFIH, two helicases and a protein kinase (23, 24). TFIH is indeed required in the postrecruitment steps along with factor TFIIE (8, 13, 25, 26). The properties of these TFIH activities may be discussed in terms of the use of ATP in the postrecruitment pathway.

The available data give strongest support to the involvement of the TFIH kinase in clearance and weakest support for the involvement of TFIH helicases in the initial opening. The involvement of the kinase in clearance is supported by diverse experiments (Refs. 2, 14, and 15; but see Refs. 27 and 28). The $K_m$ value for the use of ATP in a protein kinase assay was found to be 40 $\mu$M for the kinase component, CAK, of TFIH (29). This is essentially identical to the $K_m$ measured here for the pro-
moter clearance reaction, lending additional support to the involve-
ment of the TFIH kinase in promoter clearance.

By contrast, there is very poor agreement between the $K_m$ values measured here for POC and IOC formation and that for the TFIH helicases. The $K_m$ value measured for the TFIH “transcription” helicase is approximately 200 $\mu$M (30–32), which is in the typical range for helicases (17). This is 20–50 times higher than the values found here for initial opening and subsequent extension and stabilization. The contrast is sup-
ported by prior experiments reporting very low $K_m$ values for formation of sarkosyl-resistant initiated complexes (5). The
contradiction is not definitive, because the $K_m$ value for a helicase in a replication system can be dramatically reduced in the context of a larger macromolecular complex (33). An ATPase activity within TFIIH with a low $K_m$ value has been reported, and its coupling to helicase activity was implied (34). Thus, these considerations suggest that TFIIH could be involved, but they do not identify the appropriate activity within it.

Other data support some involvement of the TFIIH transcription helicase. The helicase subunit has been mutated, and the re-assembled TFIIH was shown to be deficient in reaching the stage of a fully extended stable open complex (IOC formation) (13). Initial opening (POC formation) was not assayed. Thus, TFIIH is required to reach the IOC stage in this system. The mutations destroyed the presumptive ATP binding sites of the polypeptide and thus inactivated the associated ATP-dependent helicase activity. This helicase is known to be involved in DNA repair and is a typical repair helicase in that it uses templates at which melting has been initiated by mispairing and then extends the length of the melted region. This activity is analogous to the transition from POC to IOC, where a melted bubble as in a typical helicase reaction. Presumably, single strand DNA binding activities within the transcription machinery would be used to stabilize the open complexes. To be fully harmonious with the data of this report, the helicase activity would need to be assisted by the formation of a DNA-RNA hybrid with a length of at least 3 base pairs. Whether or not this speculation proves to be correct, the data presented here should provide significant constraints on any models proposed.

Acknowledgment—We thank members of the Gralla laboratory for comments on the manuscript.

REFERENCES

1. Roeder, R. G. (1996) Trends Biochem. Sci. 21, 327–335
2. Jiang, Y., Yan, M., and Gralla, J. D. (1996) Mol. Cell. Biol. 16, 1614–1621
3. Bunick, D., Zandomeni, R., Ackerman, S., and Weinmann, R. (1982) Cell 29, 877–888
4. Sawadogo, M., and Roeder, R. G. (1984) J. Biol. Chem. 259, 5321–5326
5. Conaway, R. C., and Conaway, J. W. (1988) J. Biol. Chem. 263, 2926–2968
6. Wang, W., Carey, M., and Gralla, J. D. (1992) Science 255, 450–453
7. Jiang, Y., Snaile, S. T., and Gralla, J. D. (1993) J. Biol. Chem. 268, 6535–6540
8. Goodrich, J. A., and Tjian, R. (1994) Cell 77, 145–156
9. Dvir, A., Conaway, R. C., and Conaway, J. W. (1996) J. Biol. Chem. 271, 23552–23556
10. Holstege, F. C., Fiedler, U., and Timmers, H. T. (1997) EMBO J. 16, 7468–7480
11. Yan, M., and Gralla, J. D. (1997) EMBO J. 16, 7457–7467
12. Holstege, F. C., van der Vliet, P. C., and Timmers, H. T. (1996) EMBO J. 15, 1666–1677
13. Tirode, F., Busso, D., Coin, F., and Egly, J. M. (1999) Mol. Cell 3, 87–95
14. Yankulov, K. Y., Pandes, M., McCracken, S., Bouchard, D., and Bentley, D. L. (1996) Mol. Cell. Biol. 16, 3291–3299
15. Akoulitchev, S., Makela, T. P., Weinberg, R. A., and Reinberg, D. (1995) Nature 377, 557–560
16. Gebara, M. M., Sayre, M. H., and Corden, J. L. (1997) J. Cell. Biochem. 64, 390–402
17. Matson, S., and Kaiser-Rogers, K. A. (1990) Annu. Rev. Biochem 59, 289–329
18. Carey, M., Leatherwood, J., and Ptashne, M. (1990) Science 247, 710–712
19. Jiang, Y., Yon, M., and Gralla, J. D. (1995) J. Biol. Chem. 270, 27332–27338
20. Jiang, Y., and Gralla, J. D. (1995) J. Biol. Chem. 270, 1277–1281
21. Dvir, A., Garrett, K. P., Chalut, C., Egly, J. M., Conaway, J. W., and Conaway, R. C. (1996) J. Biol. Chem. 271, 7245–7248
22. Wolner, B. S., and Gralla, J. D. (1997) J. Biol. Chem. 272, 32301–32307
23. Serizawa, H., Conaway, R. C., and Conaway, J. W. (1992) Proc. Natl. Acad. Sci. U. S. A. 89, 7476–7480
24. Schaeffer, L., Moncolin, V., Roy, R., Staub, A., Mezzina, M., Sarasin, A., Weeda, G., Hoeijmakers, J. H., and Egly, J. M. (1994) EMBO J. 13, 2388–2392
25. Ohkuma, Y. (1997) J. Biochem. (Tokyo) 122, 481–489
26. Dvir, A., Tan, S., Conaway, J. W., and Conaway, R. C. (1997) J. Biol. Chem. 272, 28175–28178
27. Kugel, J. F., and Goodrich, J. A. (1998) Proc. Natl. Acad. Sci. U. S. A. 95, 9232–9237
28. Dvir, A., Conaway, R. C., and Conaway, J. W. (1997) Proc. Natl. Acad. Sci. U. S. A. 94, 9006–9010
29. Solomon, M. J., Harper, J. W., and Shattilworth, J. (1993) EMBO J. 12, 3133–3142
30. Serizawa, H., Conaway, R. C., and Conaway, J. W. (1993) J. Biol. Chem. 268, 17300–17308
31. Sung, P., Bally, V., Weber, C., Thompson, L. H., Prakash, L., and Prakash, S. (1993) Nature 365, 852–855
32. Schaeffer, L., Roy, R., Humbert, S., Moncolin, V., Vermeulen, W., Hoeijmakers, J. H., Chambon, P., and Egly, J. M. (1993) Science 260, 58–63
33. Kornberg, A., Scott, J., and Bertsch, L. (1978) J. Biol. Chem. 253, 3288–3304
34. Conaway, R. C., and Conaway, J. W. (1989) Proc. Natl. Acad. Sci. U. S. A. 86, 7356–7360
35. Volankar, S. S., Soultanas, P., Dillingham, M. S., Subramanya, H. S., and Wigley, D. B. (1999) Cell 97, 75–84
36. Guo, Y., and Gralla, J. D. (1998) Proc. Natl. Acad. Sci. U. S. A. 95, 11655–11660
The Use of ATP and Initiating Nucleotides during Postrecruitment Steps at the Activated Adenovirus E4 Promoter

Ming Yan and Jay D. Gralla

J. Biol. Chem. 1999, 274:34819-34824.
doi: 10.1074/jbc.274.49.34819

Access the most updated version of this article at http://www.jbc.org/content/274/49/34819

Alerts:
• When this article is cited
• When a correction for this article is posted

Click here to choose from all of JBC's e-mail alerts

This article cites 36 references, 23 of which can be accessed free at http://www.jbc.org/content/274/49/34819.full.html#ref-list-1