Transcription Factor Rho Does Not Require a Free End to Act as an RNA-DNA Helicase on an RNA*

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Escherichia coli Rho factor is a ring-shaped, homohexameric protein that terminates synthesis of RNA through interactions with the nascent RNA transcript. Because its mechanism of action may involve translocation of the RNA transcript through the hole in its ring structure, its action could depend on the availability of a free 5′-end. To determine whether Rho's activity is 5′-end-dependent, its ability to bind to and function on a circular derivative of λ cro mRNA was investigated. The circular derivative was made in vitro by action of RNA ligase on a derivative of λ cro RNA containing an extra 10-nucleotide sequence near the 5′-end that was complementary to a sequence located near the 3′-end. Rho bound nearly as tightly to the circular derivative RNA as to the standard cro transcript. Rho was also able to readily dissociate a DNA oligonucleotide from its helical complex with the circular RNA in an ATP-dependent reaction. Thus, the action of Rho on a transcript does not depend on the availability of a free 5′-terminus.

Transcription termination factor Rho is a RNA-binding protein that couples the energy derived from ATP hydrolysis to actions that dissociate a RNA transcript from its biosynthetic complex with DNA and RNA polymerase (1, 2). Rho also can dissociate a RNA molecule bound to DNA through a short hybrid helix in a reaction that is dependent on ATP hydrolysis and the presence of an attachment site for Rho on the RNA on the 5′ side of the hybrid helix (3–5). This RNA-DNA helicase activity may mimic the process of removal of the nascent RNA strand from the transcription elongation complex.

Rho factor is believed to function in vitro as a hexamer consisting of six polypeptide subunits arranged in a ring-shaped structure (6, 7). Burgess and Richardson (8) have recently presented a model for the Rho-RNA complex in which a segment of RNA, called a run site (ρho utilization site), binds to a clasp comprised of the N-terminal RNA-binding domains of the six individual subunits located at one end of the hexameric structure (the crown) (9–11). RNA sequence 3′ of the run site then passes into the hole located at the center of the hexamer. Evidence for passage of a single-stranded nucleic acid substrate through a ring-shaped hexameric structure has been observed for other hexameric helicases, such as DnaB and the T7 gene 4 product (12, 13).

The process by which Rho binds to and captures the 3′-end of an RNA in the center of the hexamer is not known. Gan and Richardson (14) have recently presented data indicating that Rho, in vitro, could form hexamers by partial assembly of subunits on an RNA. Another mechanism could have the RNA enter into the center of the hexameric structure through an opening or notch in the ring (7). A third mechanism may involve Rho threading onto the nascent transcript from the free 5′-end of the RNA.

To test the model in which Rho requires a free end of RNA to thread onto in order to function as a terminator, we investigated Rho's ability to utilize its ATP-dependent helicase activity on an RNA lacking a free end. This can be done by using a circular RNA to test Rho's ability to disrupt RNA-DNA hybrid helices. These results indicate that Rho is indeed able to function as a helicase on an RNA lacking a free end.

**EXPERIMENTAL PROCEDURES**

Materials—All restriction enzymes, T4 RNA ligase, T4 polynucleotide kinase, and calf intestinal alkaline phosphatase were purchased from New England Biolabs, Inc. The oligonucleotides were purchased from Integrated DNA Technologies. All of the ribonucleotides were purchased from Roche Molecular Biochemicals. Radioactive nucleotides were purchased from ICN Radiochemicals. RNasin was purchased from Promega. T7 RNA polymerase and wild-type Rho were provided by Lislott Richardson (Indiana University).

pBeCro—pBCro is a derivative of pBluescript II KS(−) (15) that contains a 10-base pair insertion sequence at the 5′-end of the transcription unit for the λ cro mRNA. This derivative was prepared by polymerase chain reaction amplification of pBluescript II KS(−) with the mutagenic primers: primer 1 (5′-CGATTCTACTATAGGGATCGTAGAGCCATTACTAAGGAGGTTG-3′) and primer 2 (5′-CAAACCTCCCTGAATTGGCCTACTCCATATGTTG-3′). The resulting plasmid was sequenced to confirm the presence of the desired insert in the λ cro gene.

**T7 Transcription of Linearized pBeCro—**The pBeCro plasmid was purified from the T7 transcription reaction by linearization with the restriction enzyme Tsp45I. Subsequent purification of the DNA, followed by transcription and purification of the RNA product were done as reported by Burgess and Richardson (8).

Circulation of the Linear pBeCro RNA Transcript—The 5′-terminal triphosphate of the transcript was removed by treatment of 20 µg of RNA with 2 units of calf intestinal alkaline phosphatase in 50 µl of a solution containing 20 mM Tris-Cl, pH 7.0, 50 mM KCl, 1 mM dithiothreitol, and 40 units of RNasin for 2 h at 23 °C (16). The reaction mixture was then treated with an equal volume of phenol, followed by an equal volume of chloroform/isoamyl alcohol (24:1). The RNA was precipitated with ethanol, washed with 70% ethanol, dried, and dissolved in water.

The RNA was phosphorylated at its 5′-end by treatment with 20 units of T4 polynucleotide kinase in a 50-µl reaction volume containing 10 mM Tris acetate, pH 7.5, 10 mM magnesium acetate, 50 mM potassium acetate, 8.0 µM [γ-³²P]ATP (~1500 Ci/mmol), and 40 units of RNasin for 2 h at 23°C. The RNA was then purified by treatment with phenol, chloroform/isoamyl alcohol (24:1), and ethanol precipitation.

The 5′-labeled RNA was circularized by treatment with 25 units of T4 RNA ligase in a 50-µl solution containing 25 mM Tris-Cl, pH 7.6, 10 mM dithiothreitol, 5 mM MgCl₂, 5 mM ATP, and 0.25 µg/ml acetylated bovine serum albumin, and 40 units RNasin for 15 h at 17°C. The RNA was precipitated with ethanol; washed with 70% ethanol; dried; dissolved in 16 µl of a solution containing 98% formamide, 2 mM EDTA, 1500 Ci/mmol, and 40 units of RNasin for 2 h at 23°C. The RNA was then purified by treatment with phenol, chloroform/isoamyl alcohol (24:1), and ethanol precipitation.

The 5′-labeled RNA was circularized by treatment with 25 units of T4 RNA ligase in a 50-µl solution containing 25 mM Tris-Cl, pH 7.6, 10 mM dithiothreitol, 5 mM MgCl₂, 5 mM ATP, and 0.25 µg/ml acetylated bovine serum albumin, and 40 units RNasin for 15 h at 17°C. The RNA was precipitated with ethanol; washed with 70% ethanol; dried; dissolved in 16 µl of a solution containing 98% formamide, 2 mM EDTA, 1500 Ci/mmol, and 40 units of RNasin for 2 h at 23°C. The RNA was then purified by treatment with phenol, chloroform/isoamyl alcohol (24:1), and ethanol precipitation.
Rho Action on a Circular RNA

0.03% bromphenol blue, and 0.03% xylene cyanol; and separated by electrophoresis on a 6%, 7 M urea polyacrylamide gel (acylamide/bisacrylamide, 19:1) containing 45 mM Tris borate and 1 mM EDTA. The ligated, circularized RNA ran with a slower mobility than the unligated, linear form on this denaturing gel. Approximately 30% of the RNA in the ligation reaction was circularized. The RNA was identified by UV shadowing and excised using a sterile razor blade. The RNA was recovered as described by Burgess and Richardson (8). Concentration of the RNA was determined by its optical absorbance at 260 nm.

Filter Binding Experiments—Filter binding experiments involving both the unligated and circular derivatives of the cro RNA with wild-type Rho were performed and analyzed according to Gan and Richardson (14). All binding experiments were performed in a solution containing 40 mM Tris-HCl, pH 8.0, 10 mM MgCl₂, 50 mM KCl, 0.1 mM dithiothreitol, 0.1 mM EDTA, 1 mM ATP, and 0.25 mg/ml acetylated bovine serum albumin.

**Annexing of RNA Oligonucleotides to the RNA—** DNA oligonucleotides complementary to nucleotides 28–46 (5' oligonucleotide), 292–348 (raf oligonucleotide), and 327–348 (3' oligonucleotide) of the standard cro RNA were chosen for these helicase experiments (see Fig. 1 for sequences) The annealing reaction contained 50 mM 32P-labeled RNA, 500 nM DNA oligonucleotide, 20 mM Hepes-KOH buffer, pH 8.0, 50 mM KCl, 1 mM MgCl₂, 0.1 mM EDTA, 1 mM dithiothreitol, 0.1 mM EDTA, 1 mM ATP, and 0.25 mg/ml acetylated bovine serum albumin.

**Rho RNA-DNA Helicase Reaction—** The helicase reactions contained one-tenth volume of the annealing reaction (50 mM 5000 nM DNA oligomer), which resulted in ~4.5 mM RNA-DNA hybrid. The reactions also contained 32 mM Hepes-KOH buffer, pH 6.0, 50 mM KCl, 1 mM MgCl₂, 0.1 mM EDTA, 1 mM dithiothreitol, 40 units of RNasin, 0.2 mg/ml acetylated polyacrylamide gel (17); stacking gel contained 5% polyacrylamide (acylamide/bisacrylamide, 29:1), 125 mM Tris-HCl, pH 6.8, 4% SDS, 0.2% bromphenol blue, and 20% glycerol. The helicase reactions were analyzed on a discontinuous Laemmli polyacrylamide gel (18), using a stacking gel containing 25 mM Tris, 250 mM glycine, and 0.1% SDS. These gels were run at low current (11 mA) and temperature (4 °C) to prevent disruption of the RNA-DNA hybrid during electrophoresis. Following exposure of the gel to a phosphorimager plate, the data were analyzed using ImageQuant software (Molecular Dynamics, Inc., Sunnyvale, CA).

The data points relating the fraction of RNA-DNA hybrid remaining versus time for each sample were fit to the following two-phase decay equation (4),

\[
F = A_1 e^{-kt_1} + (A_2 - k_2)
\]  
(Eq. 1)

where F is the fraction RNA-DNA hybrid remaining after time t (t = 0 s was normalized to 1), A₁ and k₁ are the amplitude and rate constant (units s⁻¹), respectively, for the first fast burst (exponential) decay phase, and A₂ and k₂ are the intercept and slope, respectively, of the second slower linear-decay phase.

**RESULTS AND DISCUSSION**

To determine whether Rho could bind to and act on a transcript lacking a free 5'-end, a circular derivative of the cro RNA, a transcript that is terminated at the well characterized Rho-dependent terminator TR1 located between genes cro and clII of bacteriophage λ, was prepared. The method chosen to make a circular RNA (16) involved preparing a 391-nucleotide derivative of the λ cro RNA, which contained an inserted sequence of 10 nucleotides (between nucleotides 6 and 5 in the wild-type cro RNA sequence) that were complementary to a 10-nucleotide sequence near the 3’-end of the RNA (nucleotides 366–375). With this extra sequence, the RNA can form a stable stem helix, which would bring the 5' - and 3' - ends into close proximity. After converting the 5'-triphosphate of the primary transcript to a monophosphate, treatment of this RNA with T4 RNA ligase converted ~30% of the RNA to a circular form. The ligated, circular RNA was separated from the unligated RNA because of its slower mobility during electrophoresis on a 7 M urea polyacrylamide gel.

**Rho Binds to Circular RNA—** To determine whether Rho can bind the circular cro derivative RNA, we used the nitrocellulose filter-binding technique to isolate complexes of Rho with radiolabeled RNA (15, 18). With saturating levels of Rho, ~60% of the circular cro RNA was retained on the filter. This efficiency of retention of the complex was nearly identical to that found with the standard cro RNA under the same binding conditions (14). The affinity of Rho for the RNAs was determined by measuring the fraction of RNA retained on the filter at varying concentrations of Rho and finding the best fit of these data to the equation for formation of a simple bimolecular complex between the RNA and hexameric Rho. As was shown for the standard cro RNA, the assumption that Rho bound RNA as a hexamer is a good approximation when ATP was present in the binding mixture (14). The Kₐ values determined by this procedure were: 0.03 ± 0.01, 0.07 ± 0.01, and 0.14 ± 0.03 nM for the complex with the standard cro RNA, the ligated (circular) cro derivative RNA, and unligated cro derivative RNA, respectively. Thus, Rho does not bind as tightly to the derivative cro RNAs as to the standard cro RNA, but it does bind with slightly higher affinity to the circular RNA than to its unligated precursor.

One possible reason why Rho binds with a somewhat weaker affinity to the derivative RNAs than to the standard cro RNA is that the formation of the stem-helix between the 3' - and 5' - ends in the derivative RNAs has changed their overall tertiary structure. These structural changes may have made the binding site on the derivative RNAs less accessible to Rho than on the standard cro RNA. In any case, these data indicate that Rho can bind to the circular RNA nearly as well as it binds to the standard cro RNA.

**Rho Exhibits ATP-dependent RNA-DNA Helicase Activity on a Circular RNA Substrate—** Rho can utilize the energy derived from ATP hydrolysis to translocate along a RNA in a 3' direction and to disrupt RNA-DNA hybrids that are 3' of the primary Rho attachment site (3, 4). To determine if Rho can perform this ATP-driven reaction on a circular RNA, a DNA oligonucleotide complementary to a sequence on the 3' side of the rut site (Fig. 1, 3' oligo) was annealed to the RNA. When separated on a polyacrylamide gel containing SDS (no urea), the circular RNA-DNA oligonucleotide complex migrated more slowly than did the free RNA (Fig. 2). Incubation of the complex with a stoichiometric amount of Rho and ATP caused a time-dependent displacement of 3' oligonucleotide from the circular RNA. 86% of the oligonucleotide was displaced within 6 min. In the absence of either Rho or ATP, less than 7% of 3' oligonucleotide was displaced within 6 min. These results demonstrate that Rho acts as a helicase on a circular RNA.

To rule out the possibility that the displacement occurred because there was sufficient contaminating nucleases present to nick a majority of the circular RNA, samples of the reaction mixture were also analyzed on a polyacrylamide gel containing 7 M urea. The results revealed that ~95% of the circular RNA retained its characteristic slower mobility on the 7 M urea polyacrylamide gel. Hence, nearly all of the circular RNA remained covalently sealed throughout the course of the helicase reaction.

**Kinetics of the RNA-DNA Helicase Reaction—** To determine whether the absence of a free end alters the rapidity by which Rho can separate RNA from a hybrid complex with a DNA oligonucleotide, the time courses for the displacement reaction for the various RNAs were determined. With the standard cro RNA, the displacement reaction had two phases. About half of
the complexes were dissociated rapidly, while the rest were dissociated at a much slower rate (Fig. 3). With the two *cro* derivatives, the initial displacement was less rapid but involved a larger fraction of the complexes. The two-phase reaction observed for these RNAs was very similar to results obtained by Walstrom et al. (5) performing similar experiments on 5′- or 3′-oligonucleotide from its complex (Table II). In contrast with the unligated *cro* RNA as the substrate in their helicase reaction. These reactions can be dissociated at a much slower rate (Fig. 3). With the two derivative RNAs due to the formation of the stem structure between the 3′- and 5′-ends in the derivative RNAs, ligated or not, makes the RNA-DNA hybrid complexes with the derivative RNAs were poorer substrates for helix displacement by Rho in the initial burst phase reaction than the complexes with the standard *cro* RNA.

One possible explanation for differing rates of the initial burst phase between the standard *cro* RNA and the derivative RNAs is that formation of the stem structure between the 3′- and 5′-ends of the transcript that was involved in the helicase reaction (Fig. 1). After a 6-min incubation of the hybrid complex with ATP and a stoichiometric amount of Rho, 44% of the 5′ oligonucleotide was removed from the circular RNA as compared with 71% of the 3′ oligonucleotide from its complex (Table II). In contrast with the unligated *cro* RNA, only 12% of the 5′ oligonucleotide was displaced, whereas again 71% of the 3′ oligonucleotide was displaced. On the ligated, circular *cro* RNA, the 5′ oligonucleotide was located further downstream (54 nucleotides) from the *rut* site than the 3′ oligonucleotide was in its complex. In contrast, for both of the *cro* derivatives, about 80% of the complexes were dissociated in the burst phase; however, the rates (~0.03 s⁻¹) were about 10-fold slower than the rate determined for the standard *cro* RNA. The small fraction of complexes remaining for both of the derivative *cro* RNAs were dissociated with a *k₂* of ~5 × 10⁻⁴ s⁻¹. These results indicate that the RNA-DNA hybrid complexes with the derivative *cro* RNAs were poorer substrates for helix displacement by Rho in the initial burst phase reaction than the complexes with the standard *cro* RNA.

**Fig. 3.** Kinetics of displacement of the 3′ oligonucleotide from the various *cro* RNA transcripts by Rho's helicase activity. Reactions contained 4.5 nm hybrid helix and 5 nm Rho hexamer and were initiated by the addition of 1 mM ATP at 37 °C. Aliquots of the reaction were taken at 15, 45, 90, 180, and 360 s and were immediately mixed with a buffer containing 0.1% SDS, which quenched the reaction by denaturation of Rho. All samples were separated by electrophoresis on a 5% polyacrylamide gel with 0.1% SDS at 4 °C. Open squares, standard *cro* RNA; open circles, unligated *cro* derivative RNA; closed circles, circular *cro* derivative RNA. Reactions were analyzed by exposure of the gel to a PhosphorImager plate and were quantitated using ImageQuant (Molecular Dynamics) and Grafit 3.03 (Erithacus Software Ltd.) software.
addition, the 5′ oligonucleotide hybrid was downstream of the stem structure that brought the 3′- and 5′-ends together for ligation. Both of these conditions are likely reasons why the 5′ oligonucleotide was removed less efficiently than the 3′ oligonucleotide from the circular cro RNA. On the other hand, the much lower displacement of the 5′ oligonucleotide from the unligated derivative RNA containing the same stem structure demonstrates a dependence on the covalent continuity of the RNA across this segment of RNA for the improved efficiency of displacement. This is thus further evidence that Rho can function on a circular RNA.

This result with the unligated cro derivative is also consistent with other observations that Rho will not displace a hybrid that is on the 5′ side of the rut sequence. This latter observation is important because of the unexpected finding that Rho was able to displace as much as 30% of the 5′ oligonucleotide within 6 min (Table II) from a complex with this oligonucleotide hybridized to the standard cro RNA. The reason for this partial but significant level of displacement is unknown. However, the displacement was dependent on the presence of both Rho and ATP, since less than 2% of this hybrid was displaced from the standard cro RNA or either of the cro derivatives when incubated with either ATP or Rho alone for 6 min (data not shown).

In all of the previous cases in which there was little or no displacement of an upstream DNA hybrid, the 5′-end of the RNA transcript was in a double helical structure. In experiments with trpC′ RNA (3, 4), the upstream hybrid was at the 5′-end and in our experiment with the unligated cro derivative RNA, the 5′-end was in a helical stem with the 3′-end of the transcript. In contrast to those RNAs, the standard cro RNA had a 5′ RNA segment of 28 nucleotides that could provide Rho access to an upstream hybrid from the 5′ side. Because the amount of Rho was stoichiometric with the amount of RNA under the conditions used, most, if not all, of the Rho molecules would be bound to the rut segment of the cro RNA (19). In this case, an interaction of the 5′-end of an RNA with the hybrid dissociation site in Rho could occur by looping of the same RNA into the site or by action on a second, separate RNA molecule.

To investigate the importance of the rut site to Rho action, the rut oligonucleotide was used to block the beginning of the rut site for all three RNAs. Faus and Richardson (15) showed that blocking this portion of the rut site with an oligonucleotide inhibited Rho’s ability to bind to cro RNA. Also, Chen et al. (20) showed that blocking the rut site with a similar DNA oligonucleotide inhibited Rho’s in vitro termination activity at the trl terminator of the λ cro gene. As expected from these prior observations, Rho displaced less than 7% of the rut oligonucleotide from the complexes with any of the three cro RNAs (Table II). These results also provide further evidence that the helicase activity is a faithful representation of Rho’s action in transcription termination.

**Implications for Rho’s Function in Vivo**—According to a recent model of Rho-RNA interaction presented by Burgess and Richardson (8), Rho is believed to initially bind to a loading site located on the RNA transcript through interactions in a cleft located around the crown of the hexameric structure, composed of the N-terminal RNA-binding domains of the individual subunits of Rho. Following this primary RNA binding event, RNA is then passed into the center of the ring. The mechanism for this transit is unknown. From these results, a mechanism that requires Rho to thread onto a free 5′-end of the RNA for function is unlikely. Other possible mechanisms include either passage of the RNA through an opening of a notched form of the hexamer (as seen in electron micrographic images of Rho) (6, 7) or through an opening caused by partial disassembly of the hexamer on the RNA (14). In its normal context at the end of an operon, a Rho-dependent terminator would encode a rut segment that would be located downstream of the translated segment of the RNA. In order for Rho to load onto this RNA, it must be able to bind an

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### Table I

**Values of parameters from best fit curves of Rho’s RNA-DNA helicase reaction**

Parameters are from data fit to Equation 1. The curves fit to these data are shown in Fig. 3. The values shown are the parameters from the data that were averaged from two experiments per RNA.

| cro RNA form | Burst phase | Slow linear phase |
|--------------|-------------|-------------------|
|              | A1 †         | k1 †              | A2 ‡         | k2 ‡              |
| Standard     | 0.38 ± 0.01  | 0.28 ± 0.008     | 0.62 ± 0.14  | 0.0008 ± 0.0003  |
| Unligated derivative | 0.77 ± 0.05  | 0.03 ± 0.004     | 0.25 ± 0.05  | 0.0003 ± 0.0002  |
| Circular derivative | 0.76 ± 0.06  | 0.03 ± 0.006     | 0.26 ± 0.06  | 0.0001 ± 0.0002  |

† Amplitude, or fraction of RNA-DNA hybrids disrupted during the burst phase.
‡ Rate constant for burst phase.
‡ y intercept of the slow linear phase.
‡ Rate constant for slow linear phase (fraction RNA-DNA hybrids disrupted s⁻¹).

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### Table II

**Characterization of Rho’s helicase activity using DNA oligonucleotides annealed to different locations on the various λ cro RNA transcripts**

All reactions were performed using 4.5 mM RNA-DNA hybrid and 5 mM Rho hexamer at 37 °C. All reactions were initiated by the addition of 1 mM ATP to mixtures preincubated with both the RNA-DNA hybrid and Rho. Less than 2% of the hybrid complexes listed were displaced upon incubation of that complex in the presence of either Rho or ATP individually.

| cro RNA | Oligonucleotide | t = 0 min | t = 6 min | Δ |
|---------|----------------|-----------|-----------|---|
| Standard | 5′ | 0.86 ± 0.03 | 0.60 ± 0.02 | 30 |
|         | 3′ | 0.81 ± 0.04 | 0.31 ± 0.04 | 62 |
|         | rut | 0.91 ± 0.05 | 0.89 ± 0.04 | 2  |
| Unligated derivative | 5′ | 0.80 ± 0.02 | 0.70 ± 0.05 | 12 |
|         | 3′ | 0.83 ± 0.07 | 0.77 ± 0.03 | 7  |
|         | rut | 0.60 ± 0.01 | 0.18 ± 0.06 | 71 |
| Circular derivative | 5′ | 0.77 ± 0.02 | 0.43 ± 0.05 | 44 |
|         | 3′ | 0.63 ± 0.11 | 0.19 ± 0.01 | 71 |
|         | rut | 0.80 ± 0.03 | 0.79 ± 0.01 | 1  |
RNA from which the 5'-end would be blocked by co-translating ribosomes and the 3'-end would be blocked by the RNA polymerase. Thus, Rho would have to bind by a mechanism that is not dependent on the availability of a free end. A similar constraint would apply to the loading of Rho onto an RNA segment downstream of a ribosome stalled on a nascent RNA during amino acid starvation, as happens for the functioning of latent intragenic terminators under starvation conditions (21). Thus, these results with the circular RNA are consistent with the expected mechanism of Rho action in the cell.

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