Escherichia coli F_1-ATPase Can Use GTP-Nonchaseable Bound Adenine Nucleotide To Synthesize ATP in Dimethyl Sulfoxide†

Seelochan Beharry and Philip D. Bragg*

Department of Biochemistry, University of British Columbia, 2146 Health Sciences Mall, Vancouver, British Columbia, Canada V6T 1Z3

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ABSTRACT: *Escherichia coli* F_1-ATPase contained 3 mol of tightly-bound adenine nucleotide/mol enzyme. A further 3 mol could be loaded by incubation of the enzyme with ATP. The unloaded enzyme was designated as a $F_1[2,1]$ type on the basis of the ability of GTP to displace 1 mol of adenine nucleotide/mol of F_1 [Kironde, F. A. S., & Cross, R. L. (1986) *J. Biol. Chem. 261*, 12544–12549]. The loaded enzyme was designated $F_1[3,3]$ since GTP could displace 3 of the 6 mol of bound adenine nucleotide/mol of F_1. Incubation of $F_1[2,1]$, $F_1[2,0]$, and $F_1[3,0]$ with phosphate in the presence of 30% (v/v) dimethyl sulfoxide led to the synthesis of ATP from endogenous bound ADP. Hydrolysis of newly synthesized ATP occurred on transfer of the F_1 from 30% (v/v) dimethyl sulfoxide to an entirely aqueous medium. Thus, synthesis and hydrolysis of ATP can occur at GTP-nonchaseable adenine nucleotide binding sites, and these sites in dimethyl sulfoxide are not necessarily equivalent to noncatalytic sites.

Escherichia coli F_1F_o, the proton-translocating ATP synthase, is the terminal enzyme of oxidative phosphorylation in which process it synthesizes ATP from ADP and inorganic phosphate. F_1[1] may be separated from F_o as a soluble enzyme able to hydrolyze ATP to ADP and phosphate (Senior, 1988; Futai et al., 1989; Penefsky & Cross, 1991). F_1 can be induced to form ATP in the presence of organic solvents such as dimethyl sulfoxide (Sakamoto & Tonumura, 1983; Yoshida, 1983; Sakamoto, 1984a,b; Cross et al., 1984; Gomez-Puyou et al., 1986; Yoshida & Allison, 1986; Kandpal et al., 1987; Beharry & Bragg, 1991a,b, 1992a,b). These systems provide useful models in which to study the mechanism of ATP synthesis.

F_1, when isolated, usually contains 3 mol of adenine nucleotide/mol of F_1 (Maeda et al., 1976; Bragg & Hou, 1977). Three other nucleotide-binding sites are present which may be filled with nucleotide by incubating F_1 with exogenous nucleotides (Wise et al., 1984; Bragg et al., 1982; Bragg, 1984; Issartel et al., 1986; Lunardi et al., 1981; Wise et al., 1981). In this respect the *E. coli* F_1 resembles enzymes from other organisms (Cross & Nalin, 1982; Nalin & Cross, 1982; Kironde & Cross, 1986, 1987; Cunningham & Cross, 1988; Grubmeyer & Penefsky, 1981a,b; Grubmeyer et al., 1982; Cross et al., 1982). Perlin et al. (1984) showed that of the six nucleotide-binding sites three were specific for adenine nucleotides whereas the remaining three sites could also bind guanine or inosine nucleotides. Kironde and Cross (1986, 1987) have shown with mitochondrial F_1 that the enzyme as isolated contains 2 mol of adenine nucleotide bound at adenine nucleotide-specific sites and 1 mol of adenine nucleotide bound at a nucleotide-nonspecific site, from which it may be displaced by GTP. They introduced the symbol $F_1[2,1]$ to describe this state of site occupancy. The site occupancy of the *E. coli* F_1 has not yet been determined.

It is generally assumed that the adenine nucleotide-specific sites are noncatalytic sites and that ATP synthesis or hydrolysis occurs at the nonspecific sites which can bind guanosine or inosine nucleotides. This view is supported by the ability of F_1 to hydrolyze GTP and ITP as well as ATP (Cross & Nalin, 1982; Nalin & Cross, 1982; Kironde & Cross, 1986, 1987; Cunningham & Cross, 1988; Perlin et al., 1984; Dunn & Futai, 1980). In the present paper we show that the definition of adenine nucleotide-specific and -nonspecific sites as being noncatalytic and catalytic sites, respectively, does not hold under all conditions.

We show that $F_1[2,1]$, $F_1[2,0]$, and $F_1[3,0]$ can all be induced to synthesize ATP from phosphate and endogenous ADP in Me_2SO.

MATERIALS AND METHODS

The F_1-ATPase of *E. coli* ML308-225 was prepared and stored as described previously (Beharry & Bragg, 1992b). ATPase assays, ATP synthesis on F_1, measurements of bound ATP and ADP with luciferin/luciferase, and protein concentration were as described before (Beharry & Bragg, 1991a,b, 1992a,b). The M_r of F_1 used in calculations was 381 000 (Senior, 1988). The $F_1[3,0]$ and $F_1[2,0]$ enzyme forms were prepared as described by Cunningham & Cross (1988).

GTP-Chase Experiments. The GTP-chase experiments were performed in two ways. In the usual way, GTP (1 mM, final concentration) was added to the reaction mixture containing 0.1 M Tris-HCl (pH 6.8), 4 mM $MgCl_2$, and 4 mM phosphate, with or without 30% (v/v) Me_2SO, before the addition of the enzyme. The mixture was then incubated for 5 min before centrifugation through the appropriate buffer-equilibrated columns of Sephadex G-50-80 (Beharry & Bragg, 1992b). In the other procedure, where indicated, the reaction mixture with F_1 in Tris/Mg^{2+}/phosphate buffer, with or without Me_2SO, was incubated for the indicated time, 5 or 30 min unless otherwise stated. Three 100-μL aliquots of the reaction mixture were centrifuged through 1-mL columns of Sephadex G50-80. The centrifugates were pooled and the volume made up to 300 μL, if necessary. GTP-Mg^{2+} (1 mM final concentration) was now added to the pooled centrifugate, and the mixture incubated for 5 min before centrifugation through 1-mL columns of Sephadex G-50-80, as before. The

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[1] Abbreviations: F_1, F_1-ATPase protein of *Escherichia coli* F_1F_o ATP synthase; Me_2SO, dimethyl sulfoxide.

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Table I: Adenine Nucleotide Content and Deduced Site Occupancy of Preloaded and Non-Preloaded F_1

	enzyme type[a]	time of incubation (min)	GTP-Mg^{2+} chase[b]	mol bound/mol of F_1 ATP	ADP	total	deduced site occupancy[c]
A							
1.	not preloaded	1	−	0.27 ± 0.04	2.9 ± 0.2	3.2 ± 0.2	[2,1]
2.	not preloaded	5	+	0.22 ± 0.02	1.7 ± 0.1	1.9 ± 0.1	
B							
3.	preloaded	1	−	0.23 ± 0.02	5.8 ± 0.3	6.0 ± 0.3	[3,3]
4.	preloaded	5	+	0.06 ± 0.01	3.0 ± 0.2	3.1 ± 0.2	

[a] Desalted F_1 (1 mg/mL) nucleotide preloaded or not preloaded, was incubated in a buffer consisting of 100 mM Tris-acetate, pH 6.8, 4 mM $MgCl_2$, and 10 mM phosphate. Samples were removed at the stipulated time, passed through a centrifuged column of Sephadex G-50-80 and heat-denatured, and the amount of ADP and ATP was measured. [b] In the GTP-chase experiments, incubation of the mixture with 1 mM GTP was for 5 min before centrifugation through Sephadex G-50-80. F_1 was preloaded with ADP by incubation with 250 μM ATP in 100 mM Tris-acetate, pH 6.8. Mg^{2+} was not added. [c] Site occupancy: [nonexchangeable nucleotide sites/mol of F_1, exchangeable sites/mol of F_1].

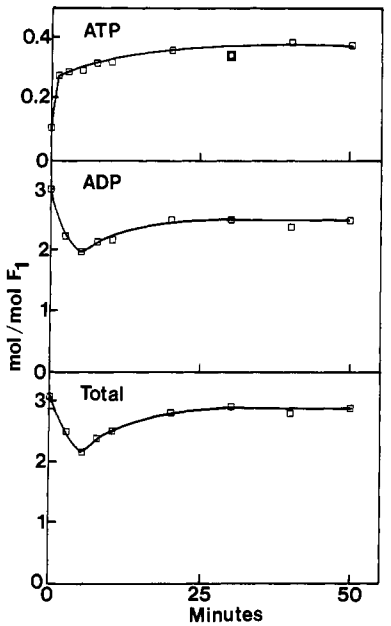

FIGURE 1: Changes in the concentration of bound adenine nucleotides in F_1[2,1] during incubation in phosphate buffer containing 30% (v/v) Me_2SO. The experiment was performed as described in Materials and Methods. Total: ATP + ADP.

ATP and ADP content of F_1 in the centrifugate was determined.

RESULTS

Nucleotide-Binding-Site Occupancy of Isolated E. coli F_1. The adenine nucleotide-specific- and -nonspecific-site occupancy of isolated *E. coli* F_1 was determined by the procedure of Cross and co-workers (Kironde & Cross, 1986, 1987; Cunningham & Cross, 1988). Adenine nucleotide bound at nonspecific sites was removed by incubation with excess GTP. *E. coli* F_1 was analyzed as isolated and after preloading the unfilled nucleotide-binding sites by a brief exposure of the F_1 to ATP (Kandpal et al., 1987; Beharry & Bragg, 1992a,b). As shown in Table I, unloaded F_1 contained 3 mol of bound adenine nucleotide. One mole of nucleotide/mole of F_1 was readily removed by GTP. The isolated enzyme is thus defined as F_1[2,1]. By the same criterion, the preloaded enzyme is F_1[3,3].

ATP Synthesis by F_1[2,1] in Me_2SO. *E. coli* F_1 was incubated in 30% (v/v) Me_2SO with Mg^{2+} and inorganic phosphate, but without added adenine nucleotide. Changes in the concentrations of bound ADP and ATP with time were measured (Figure 1). As we have observed previously with mitochondrial F_1 and with adenine nucleotide preloaded *E. coli* F_1 (Beharry & Bragg, 1992a,b), there was an initial loss of 1 mol of nucleotide/mol of F_1 over the first 2–5 min followed by rebinding. The nucleotide remaining bound during this period is present at GTP-nonchaseable (=adenine nucleotide-specific) sites (see below). ATP formation from endogenous ADP occurred rapidly, being almost complete within the first minute.

The nucleotides were released from the enzyme by heating it at 70 °C for 10 min (Beharry & Bragg, 1991a). This method is ideal for multiple samples. Denaturation of the small samples (100 μL) occurs rapidly. To check that loss of ATP by hydrolysis during the denaturation period did not occur, the amount of bound ATP released by heat denaturation was compared with that liberated by denaturation with 0.25 M perchloric acid. F_1[2,1] was allowed to synthesize ATP for 60 min in 30% (v/v) Me_2SO. The amount of bound ATP was 0.95 ± 0.05 mol/mol of F_1 determined after perchloric acid denaturation and 0.96 ± 0.03 mol/mol of F_1 determined after heat denaturation. The level of bound ADP was 1.86 ± 0.06 and 1.80 ± 0.02 mol/mol of F_1, respectively. Thus, hydrolysis of bound ATP does not occur during heat denaturation and this method is satisfactory for the release of bound nucleotide.

ATP Synthesis by F_1[2,0] and F_1[3,0] in Me_2SO. Since ATP formation had been largely completed by the time the F_1[2,0] enzyme was formed in the experiment described in Figure 1, we examined the ability of preformed F_1[2,0] to synthesize ATP in Me_2SO (Figure 2). F_1[2,0] was prepared by removal of adenine nucleotide from the nonspecific site with GTP-Mg^{2+} followed by removal of the bound guanosine nucleotide by treatment of the enzyme with 50 mM phosphate. Rapid ATP synthesis from endogenous adenine nucleotide was observed in Me_2SO. Loss and rebinding of nucleotide was not detected. Analogous data were obtained with F_1[3,0]. ATP synthesis from endogenous ADP occurred without detectable loss and rebinding of adenine nucleotide (Figure 3).

ATP Synthesis at Adenine Nucleotide-Specific Sites. The results of Figures 2 and 3 indicated that ATP synthesis in Me_2SO occurred at adenine nucleotide-specific, that is GTP-nonexchangeable, sites. This conclusion was supported by the results of the experiment shown in Table II. F_1[2,0] was incubated in Me_2SO with Mg and phosphate. At 5 and 30 min, samples were removed and passed through a small column of Sephadex G-50-80 (Beharry & Bragg, 1991a,b, 1992a,b) equilibrated with aqueous or Me_2SO-containing buffer. The samples were either analyzed for bound nucleotides or were incubated with GTP for 5 min before being passed through a second column of Sephadex G-50-80 equilibrated with the appropriate buffer. Experiments 1 and 2 of Table II confirmed that the starting enzyme was F_1[2,0]. Experiments 1, 3, and 6 showed that ATP was formed from endogenous ADP in the

Table II: Adenine Nucleotide Content of F_1[2,0] Incubated with Phosphate in the Absence and Presence of 30% (v/v) Me_2SO[a]

	buffer for				mol bound/mol of F_1		
	incubation	centrifuge column	time of incubation (min)	GTP chase	ATP	ADP	total
1.	aqueous	aqueous	1	–	0.02 ± 0.002	2.2 ± 0.2	2.2 ± 0.2
2.	aqueous	aqueous	1	+	0.01 ● 0.001	1.9 ± 0.1	1.9 ● 0.1
3.	Me_2SO	Me_2SO	5	–	0.19 ± 0.01	2.0 ● 0.1	2.2 ± 0.1
4.	Me_2SO	aqueous	5	+	0.05 ● 0.001	1.7 ± 0.1	1.75 ● 0.1
5.	Me_2SO	Me_2SO	5	+	0.17 ± 0.01	1.9 ● 0.1	2.1 ± 0.1
6.	Me_2SO	Me_2SO	30	–	0.19 ± 0.03	2.01 ± 0.03	2.20 ● 0.03
7.	Me_2SO	aqueous	30	+	0.02 ± 0.002	1.7 ± 0.3	1.7 ● 0.3
8.	Me_2SO	Me_2SO	30	+	0.22 ± 0.001	1.75 ± 0.04	1.97 ± 0.04

[a] F_1[2,0] was prepared as described by Cunningham & Cross (1988). Incubation with phosphate in the presence and absence of Me_2SO is described in Materials and Methods. The F_1 was separated from the incubation buffer by centrifugation through a column of Sephadex G-50-80 equilibrated with the indicated buffer. Selected samples were then treated with GTP as described in Materials and Methods, and F_1 was prepared for nucleotide analysis by centrifugation through a column of Sephadex G-50-80 equilibrated with the same type of buffer used before.

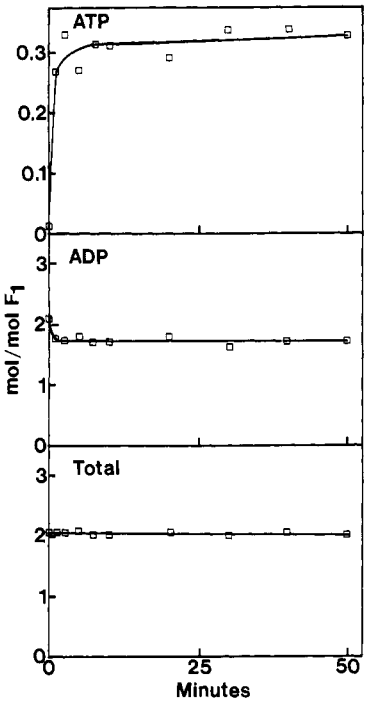

FIGURE 2: Changes in the concentration of bound adenine nucleotides in F_1[2,0] during incubation in phosphate buffer containing 30% (v/v) Me_2SO. F_1[2,0] was prepared and the experiment performed as described in Materials and Methods. Total: ATP + ADP.

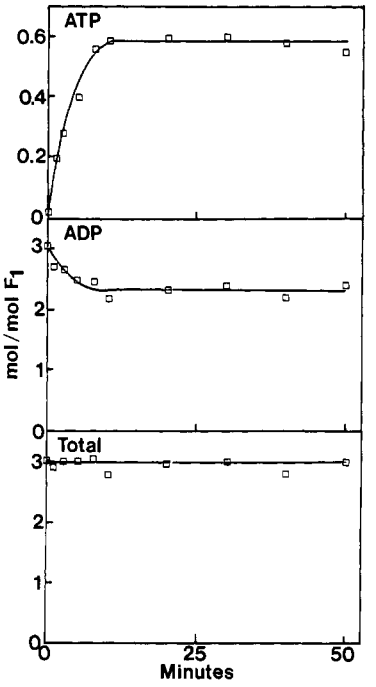

FIGURE 3: Changes in the concentration of bound adenine nucleotides in F_1[3,0] during incubation in buffer containing 30% (v/v) Me_2SO. F_1[3,0] was prepared and the experiment performed as described in Materials and Methods.

presence of 30% (v/v) Me_2SO. This ATP was not released when the enzyme was subsequently treated with GTP provided that the system was kept in 30% Me_2SO (experiments 5 and 8). However, if the enzyme was transferred to a completely aqueous system before treatment with GTP (experiments 4 and 7), the newly synthesized ATP was hydrolyzed or lost from the enzyme.

The possibility that newly synthesized ATP could be displaced by GTP when the enzyme had been transferred from Me_2SO into aqueous medium suggested that ATP synthesis might be occurring at adenine nucleotide-nonspecific sites in F_1[2,1] contaminating the F_1[2,0]. This was examined in the experiments shown in Table III (parts A and B) using F_1[2,1]. Lines 1 and 2 of Table III (part A) show that GTP treatment removed approximately 1.3 mol ADP/mol F_1. Line 3 shows that synthesis of ATP occurred in Me_2SO medium. The newly-synthesized ATP was not displaced by GTP although approximately 0.7 mol of ADP/mol of F_1 was lost (line 4). Transfer of F_1 from 30% Me_2SO to the aqueous medium resulted in disappearance of the ATP (line 5). About 0.6 mol of ADP/mol of F_1 was displaceable by GTP (line 6). Table III (part B) shows a somewhat similar experiment. In this experiment, the enzyme is equilibrated in aqueous or Me_2SO media for the appropriate time before being passed through Sephadex G-50-80 in the appropriate medium. To some samples was added GTP and the sample again passed through Sephadex G-50-80. Samples without GTP were treated similarly. Thus, experiment B differs from experiment A in that in the latter the enzyme was treated with GTP, where appropriate, before the enzyme was applied to Sephadex G-50. Lines 7 and 8 show that in F_1 transferred from 30% Me_2SO into aqueous media GTP displaces approximately 1.6 mol of ADP/mol of F_1. If the enzyme is kept in Me_2SO medium during passage through the Sephadex G-50-80 columns and during treatment with GTP, then ATP is not displaced by GTP although approximately 1.3 mol of ADP/mol of F_1 is lost from the enzyme.

Experiments 8 and 10 show that following Me_2SO treatment and two successive column centrifugations, with or without Me_2SO, the GTP chase resulted in the retention by F_1 of only 1 mol of adenine nucleotide/mol of F_1. This is reminiscent of the results of Yoshida and Allison (1986), who showed that ATP formation in Me_2SO could occur with a thermophilic F_1 containing a single molecule of bound ADP.

Table III: Adenine Nucleotide Content of F_1[2,1] Incubated with Phosphate in the Presence and Absence of 30% (v/v) Me_2SO[a]

	buffer for			mol bound/mol of F_1		
	incubation	centrifugation column	GTP chase	ATP	ADP	total
A						
1.	aqueous	aqueous	–	0.02 ● 0.01	2.88 ± 0.02	2.90 ± 0.02
2.	aqueous	aqueous	+	0.011 ● 0.001	1.59 ± 0.01	1.60 ± 0.01
3.	Me_2SO	Me_2SO	–	0.16 ± 0.01	2.4 ± 0.1	2.5 ± 0.1
4.	Me_2SO	Me_2SO	+	0.17 ± 0.01	1.7 ± 0.1	1.9 ● 0.1
5.	Me_2SO	aqueous	–	0.021 ● 0.001	2.72 ± 0.03	2.74 ± 0.03
6.	Me_2SO	aqueous	+	0.029 ± 0.001	2.1 ± 0.1	2.1 ± 0.1
B						
7.	Me_2SO	aqueous	–	0.10 ● 0.01	2.49 ± 0.03	2.59 ± 0.03
8.	Me_2SO	aqueous	+	0.073 ± 0.004	1.07 ± 0.06	1.14 ± 0.06
9.	Me_2SO	Me_2SO	–	0.23 ± 0.01	2.1 ± 0.2	2.3 ± 0.2
10.	Me_2SO	Me_2SO	+	0.18 ± 0.02	0.82 ± 0.06	1.00 ± 0.06

[a] Incubation with phosphate in the absence and presence of Me_2SO is described in Materials and Methods. Incubation in the aqueous and Me_2SO systems was for 1 and 30 min, respectively. In experiments 1–6, the F_1 was separated from the incubation buffer by centrifugation through a single column of Sephadex G-50-80 equilibrated with the indicated buffer. In the experiments with a GTP chase, the nucleotide was added to the incubation mixture 5 min prior to the centrifugation step. In experiments 7–10, the enzyme was separated from the incubation mixture by column centrifugation prior to the addition of GTP. After 5 min further of incubation, the F_1 was isolated for analysis by a second column centrifugation step.

The results of Table III show that the ATP synthesis observed in Me_2SO occurs at a site from which the nucleotide is not displaceable by GTP. Thus, the decrease in ATP observed when the enzyme is transferred from a Me_2SO to an aqueous medium must be due to hydrolysis of ATP. The site at which ATP is synthesized must also be capable of ATP hydrolysis.

DISCUSSION

The experiments described in this paper show that F_1[2,0], F_1[3,0], and F_1[2,1] in Me_2SO will synthesize ATP from endogenous ADP. With F_1[2,1] only, adenine nucleotide is released from the enzyme and rebound. We have observed this previously (Beharry & Bragg, 1992a,b). The present data show that the released nucleotide must be bound at adenine nucleotide-nonspecific sites. However, our major observation is that ATP can be synthesized at adenine nucleotide-specific sites. This is shown by ATP synthesis occurring with F_1[2,0] and F_1[3,0], enzymes in which the ADP is present only at specific sites. The extent of ATP synthesis in Me_2SO is generally less than 1 of mol/mol of F_1, although the amount formed is comparable to that observed by other workers (Sakamoto & Tonumura, 1983; Sakamoto, 1984a,b; Gomez-Puyou et al., 1986). Since the amount formed is less than stoichiometric, the possibility that ATP formation occurred at adenine nucleotide-nonspecific sites in F_1[2,1] contaminating our F_1[2,0] or F_1[3,0] preparations was considered. Adenine nucleotide bound at adenine nucleotide-nonspecific sites is displaceable by GTP (Cross & Nalin, 1982; Nalin & Cross, 1982; Kironde & Cross, 1986, 1987; Cunningham & Cross, 1988; Perlin et al., 1984; Dunn & Futai, 1980). ATP synthesized in Me_2SO was not removed by incubation with high levels of GTP, although ADP was displaced from the adenine nucleotide-nonspecific site of F_1-[2,1] under these conditions (Table III). We conclude that ATP synthesis and hydrolysis can occur at an adenine nucleotide-specific site.

This conclusion raises doubts about the previous definitions of the roles of the nucleotide-binding sites on F_1. It is generally accepted that F_1 contains three adenine nucleotide-specific noncatalytic sites and three adenine nucleotide-nonspecific catalytic sites (Cross & Nalin, 1982; Nalin & Cross, 1982; Kironde & Cross, 1986, 1987; Cunningham & Cross, 1988; Perlin et al., 1984; Dunn & Futai, 1980) with adenine nucleotide being displaceable from the latter by GTP. Our results show that in the presence of Me_2SO, at least one adenine nucleotide-specific binding site (also GTP nonexchangeable) is a catalytic site for synthesis and hydrolysis. Thus, the supposition that the adenine nucleotide-nonspecific binding sites (also GTP exchangeable) are the catalytic sites is not necessarily true in all circumstances.

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