Gene Activities for Ribosomal Components in *Escherichia coli* B/r

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The relative transcriptional activities of genes coding for ribosomal RNA (rRNA) and ribosomal proteins (r-proteins) at steady-state growth rates ranging from 0.65 to 2.1 doublings/h can be estimated from previous measurements of the synthesis rates of stable and unstable RNA (Pato & von Meyenburg, 1970; Nierlich, 1972*a,b*; Bremer *et al.*, 1973; Dennis & Bremer, 1973*b*, 1974*b*) and ribosomal proteins (Schleif, 1967; Dennis & Bremer, 1974*a*). Comparison of these transcriptional activities suggests that the expression of the r-protein genes and rRNA genes is controlled separately.

The synthesis of ribosomes in bacteria can be stimulated by shifting the culture from a minimal to a nutritionally enriched growth medium (Maaløe & Kjeldgaard, 1966). The stimulation results from an increase in the rates of transcription of the genes for rRNA and for ribosomal (r-) protein (rRNA: Pato & von Meyenburg, 1970; Nierlich, 1972 *a, b*; Dennis & Bremer, 1974*b*. mRNA for r-protein: P. P. Dennis, unpublished work). It is not known whether the ribosomal genes are actively regulated (i.e. under positive or negative control) or passively regulated (i.e. transcribed constitutively; Maaløe, 1969). The rate of transcription of a constitutive ribosomal gene should vary in parallel with all constitutive genes, depending only on the intracellular concentration of free, active RNA polymerase (because, by definition, a constitutive promoter has an invariant affinity for polymerase). However, known constitutive transcription of the *trp* and *lac* operons is decreased (relative to total mRNA transcription) under conditions where the transcription of ribosomal genes is increased (Rose & Yanofsky, 1972; Dalbow & Bremer, 1975). Thus constitutive transcription of ribosomal genes seems less likely than some form of active control.

Active control might be co-ordinate, where rRNA and r-protein genes are regulated in parallel, or non-co-ordinate, in which case the transcriptional activities at r-protein and rRNA promoters show quantitatively different changes. In this paper we estimate the transcriptional activities of the ribosomal genes for *Escherichia coli* B/r growing at different rates, based on recent measurements from this laboratory. The estimates suggest that the genes for rRNA and for r-protein are controlled separately. This is consistent with the idea of a two-step regulation; for example, the synthesis of r-protein may be regulated primarily and, in a second step,

free r-protein may act as a cofactor in the regulation of the rRNA-gene activity (Maaløe, 1969). Alternatively, rRNA synthesis may be the primarily regulated component and r-protein synthesis adjusted secondarily.

Distribution of Functioning Polymerase

In order to quantify the transcriptional activities of any set of genes, it is necessary to define parameters describing the distribution of functioning RNA polymerases among the various classes of genes, and relate those parameters to measurements of cellular RNA synthesis. The fraction of functioning RNA polymerase molecules engaged in the synthesis of stable (ribosomal and transfer) RNA (ψ_s) was previously defined (Bremer *et al.*, 1973; Dennis & Bremer, 1973*b*):

$$\psi_s = \frac{\text{number of stable growing RNA chains}}{\text{total number of growing RNA chains}}$$

This parameter was determined from the relative rate of stable RNA synthesis [ρ , defined as the ratio of the instantaneous synthesis rates of stable (r_s) and total RNA (r); $\rho = r_s/r$], and from the chain-elongation rates of stable RNA (c_s) and mRNA (c_m):

$$\psi_s = \frac{\rho}{\rho + (1 - \rho)(c_s/c_m)}$$

The fraction ψ_s is a measure for the transcriptional activity of the stable RNA genes relative to the transcriptional activity of all genes; it was found to increase with growth rate, similarly to ρ (Fig. 1*b*; note that if stable RNA and mRNA chains grow with equal rates, ρ and ψ_s will be identical).

The relative transcriptional activities of other classes of genes can be defined in analogy to ψ_s ; for example, ψ_m as the fraction of polymerase engaged in the synthesis of mRNA, or ψ_r , ψ_t , ψ_{rp} ,

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Fig. 1. Relative transcriptional activities (ψ) of different classes of genes as a function of bacterial growth rate

(a) Chain-elongation rate of mRNA (c_m) and stable RNA (c_s) from Dennis & Bremer (1973a); these values are used to calculate the ψ values in (b) and (c). Actually c_s (= average chain-growth rate of rRNA and tRNA) has not been measured, but c_r (rRNA chain-growth rate). As a result ψ_s may be somewhat underestimated (if the tRNA chain-growth rate is more like the mRNA chain-growth rate), but ψ_r (dotted line in Fig. 1c) is estimated correctly. (b) Upper curve: relative rate of stable RNA synthesis (ρ) from Dennis & Bremer (1973b; ●) and from Nierlich (1972b; ○). Lower curve: fraction (ψ_s) of functioning RNA polymerase engaged in the synthesis of stable RNA, calculated from the values of ρ , c_s and c_m , by using the relationship (Bremer *et al.*, 1973) $\psi_s = \rho / [\rho + (1 - \rho)(c_s/c_m)]$. (c) Relative transcriptional activities of the genes coding for rRNA, tRNA, ribosomal proteins and non-ribosomal proteins. —, ψ_s from (b) (sum of rRNA and tRNA gene activities). The partition between rRNA and tRNA (·····) was obtained by assuming that 85% of stable RNA is rRNA (Dennis, 1972). The partition between non-ribosomal and ribosomal proteins (-----) was obtained by assuming that the fraction of total mRNA that is mRNA for r-proteins is equal to the differential rate of r-protein synthesis (α_r , see Fig. 2a).

ψ_{nrp} as the corresponding fractions engaged in the synthesis of rRNA, tRNA, mRNA for ribosomal proteins and mRNA for non-ribosomal proteins. The sum of all discrete fractions is equal to unity:

$$\begin{aligned}\psi_s + \psi_m &= 1 \\ \psi_r + \psi_t + \psi_{rp} + \psi_{nrp} &= 1\end{aligned}$$

The distribution of polymerase between these discrete classes of genes is illustrated for *E. coli* B/r growing at different rates of balanced growth (Fig. 1c). It shows that, in slowly growing bacteria [succinate medium; μ (growth rate as doublings/h) = 0.67], 75% of the functioning RNA polymerase molecules are engaged in the synthesis of mRNA for non-ribosomal proteins and 25% are synthesizing rRNA, tRNA and mRNA for ribosomal proteins. In rapidly growing bacteria, these proportions are essentially reversed, indicating that, at increasingly higher growth rates, the bacterial cell devotes an increasingly greater proportion of its biosynthetic capacity to the production of ribosomes.

Transcription of RNA Genes

The transcriptional activity of rRNA genes, ψ_r , is obtained from the ratio of rRNA/stable RNA and the transcriptional activity of stable RNA genes. The rRNA represents a nearly constant fraction of stable RNA (0.85) and this fraction shows only a slight variation at growth rates above 0.6 doublings/h. Thus ψ_r is approximated by the relationship

$$\psi_r = 0.85\psi_s$$

and increases 2.5-fold from a value of 0.19 at $\mu = 0.67$, to 0.47 at $\mu = 2.1$ (Fig. 1c and Table 1).

Transcription of r-Protein Genes

The transcriptional activity of r-protein genes, ψ_{rp} , is obtained from the differential rate of r-protein synthesis (α_r) defined by Schleif:

$$\alpha_r = \frac{\text{r-protein synthesis rate}}{\text{total protein synthesis rate}}$$

Table 1. Comparison of the gene activities for ribosomal RNA (ψ_r) and ribosomal proteins (ψ_{rp}) for bacteria growing in succinate or glucose–amino acids medium

ψ_s = fraction of functioning RNA polymerase engaged in the synthesis of stable RNA (values from Dennis & Bremer, 1974b). ψ_r = fraction of functioning RNA polymerase engaged in the synthesis of ribosomal RNA [the ratio $\psi_r/\psi_s = \text{rRNA}/(\text{rRNA} + \text{tRNA})$ is nearly independent of the growth rate (Dennis, 1972) such that $\psi_r = 0.85\psi_s$]. ψ_m = fraction of functioning RNA polymerase engaged in the synthesis of total messenger RNA ($\psi_m = 1 - \psi_s$). α_r = differential rate of ribosomal protein synthesis (steady-state values from Dennis & Bremer, 1974a). The 5 min post-shift value was assumed to be equal to the post-shift steady-state value (Schleif, 1967). ψ_{rp} = fraction of functioning RNA polymerase engaged in the synthesis of mRNA for ribosomal proteins ($\psi_{rp} = \alpha_r \cdot \psi_m$).

	Growth rate (doublings/h)	Gene activities				
		ψ_s	ψ_r	ψ_m	α_r	ψ_{rp}
Succinate medium	0.67	0.22	0.19	0.78	0.085	0.066
Glucose–amino acids medium	2.10	0.55	0.47	0.45	0.190	0.085
5 min after shift from succinate to glucose–amino acids	—	0.60	0.51	0.40	(0.190)	0.76
Ratio glucose–amino acids/succinate	3.1	2.5	2.5	0.58	2.2	1.3

Fig. 2. Relative transcriptional activities of the genes for rRNA and r-protein

(a) — (right ordinate), Differential rate of r-protein synthesis (α_r), from Dennis & Bremer (1974a). The long dashes indicate that the curve extrapolates to zero at zero growth rate. ---- (left ordinate), Fraction (ψ_m) of functioning RNA polymerase engaged in the synthesis of mRNA; from the ψ_s curve of Fig. 1(b): $\psi_m = 1 - \psi_s$. (b) Relative transcriptional activities of the genes for rRNA (ψ_r) and r-proteins (ψ_{rp}); both curves are normalized by setting the values for glucose medium (1.36 doublings/h) at unity. The ψ_r curve is equivalent to the dotted line in Fig. 1(c) ($\psi_r = 0.85\psi_s$). The ψ_{rp} curve is obtained as the product $\alpha_r \cdot \psi_m$ from (a).

and from the transcriptional activity of mRNA genes, ψ_m . If translation of mRNA were indiscriminate (i.e. all mRNA species served with equal efficiency in protein synthesis) or if r-protein mRNA were translated as frequently as average mRNA, then

$$\alpha_r = \frac{\text{amount of mRNA for r-protein}}{\text{amount of total mRNA}} = \frac{\psi_{rp}}{\psi_m}$$

The transcriptional activity of r-protein genes is then related to α_r and ψ_s or ψ_m by the relationship

$$\psi_{rp} = \alpha_r \psi_m = \alpha_r (1 - \psi_s)$$

and increases only 1.3-fold from a value of 0.066 at $\mu = 0.67$, to 0.085 at $\mu = 2.1$ (Fig. 2 and Table 1). Although the absolute values of ψ_{rp} may differ by a constant factor (if r-protein mRNA were translated more or less frequently than average mRNA) this increase in ψ_{rp} is independent of the relative translational efficiencies of different mRNA species.

Transcriptional Changes after a Nutritional Shift-up

Within minutes after a shift-up from succinate to glucose–amino acids medium, the rate of ribosome synthesis (both rRNA and r-protein components)

Table 2. RNA-chain initiation at the promoters of ribosomal genes in *E. coli* B/r growing in succinate minimal medium (0.67 doubling/h, pre-shift medium), 5 min after a nutritional shift-up to glucose-amino acids medium and during steady-state growth in glucose-amino acids medium (2.14 doublings/h; post-shift medium)

Parameter	Units	Symbol	Pre-shift	5 min post-shift	Steady-state post-shift	Reference
Number of rRNA genes	Genes/genome	G_r	7.4	7.4	9.5	$G_r = 60^*$
Number of r-protein genes	Genes/genome	G_{rp}	1.2	1.2	1.6	$G_r = O^*$
Rate of synthesis of stable RNA	10^4 nucleotides/min per genome	r_s	1.7	5.3	16.9	Dennis & Bremer (1974b,c)
Relative rate of stable RNA synthesis	Ratio stable-RNA/total-RNA synthesis	ρ	0.29	0.68	0.68	Dennis & Bremer (1974b,c)
Differential rate of r-protein synthesis	Ratio r-protein/total protein synthesis rate	α_r	0.085	0.19	0.19	Dennis & Bremer (1974a)
Rate of RNA chain initiation at the rRNA promoters	Chains/min per promoter	i_r	3.8 (1.0)†	12.4 (3.3)	30.3 (8.0)	Eqn. (1b) of the Appendix, substituting the parameters above
Rate of RNA chain initiation at the r-protein promoters	Chains/min per promoter	i_{rp}	1.3 (1.0)‡	1.8 (1.4)	4.6 (3.5)	Eqn. (5b) of the Appendix and parameters above

* O = Number of chromosome origins per genome equivalent of DNA; see the Appendix.

† The numbers give the absolute and relative (normalized to the value for succinate medium = 1.0, in parentheses) initiation rates.

‡ The absolute values of i_{rp} depend on the assumption that mRNA for r-protein is translated as many times as average mRNA (see the Appendix); relative values depend on the assumption that there is no gene-specific regulation at the translational level.

increases about threefold; the increase is equivalent to the ratio of the post-shift/pre-shift steady-state growth rates (Schleif, 1967). The abrupt increase in the synthesis rates of ribosomal components is accompanied by changes in the transcriptional activities of rRNA and r-protein genes which occur during the initial 5 min after the shift (Tables 1 and 2). The difference between the threefold increase in the synthesis rate of r-protein and the 1.3–1.4-fold increase in the transcriptional activity of the r-protein genes reflects a more efficient utilization of mRNA at higher growth rates (i.e. in the post-shift medium mRNA molecules are translated more frequently and the ribosomes are packed more densely on the mRNA molecules; Dennis & Bremer, 1974c). Measurements of r-protein mRNA by DNA-RNA hybridization showed that the amount of r-protein mRNA after the shift increases twofold (P. P. Dennis, unpublished work), whereas we estimate here a 1.4-fold increase in the rate. The difference may reflect an increase in the chemical life of mRNA.

Adjustments late after the shift-up

The ratio of the rate of synthesis of rRNA to that for mRNA, and similarly the fractions ψ_r and ψ_m , reach their post-shift steady-state values within a few minutes after a shift-up (Pato & von Meyenberg, 1970; Nierlich, 1972; Dennis & Bremer, 1974b).

Two further parameters which are expected to influence gene expression, the ribosomal gene dosage (number of rRNA and r-protein genes per genome equivalent of DNA) and the concentration of free (functional) RNA polymerase molecules, increase only gradually to their post-shift steady-state values. Changes in these latter parameters are responsible for the late post-shift changes in the rate of RNA-chain initiation (2.5-fold further increase) at the ribosomal gene promoters (Table 2).

Rates of Transcription Initiation

The activity of particular genes was expressed here by the fraction (ψ) of (total) transcribing RNA polymerase that is engaged in the transcription of these genes. Other parameters may be used to express gene activities which require different measurements for their determination (see the Appendix). The most direct measure for gene activity is the rate of RNA-chain initiation at the gene promoter (Table 2). In some instances, the initiation rate may tell less than ψ about the regulatory state of the promoter; for example, by lowering the temperature of the growth medium, the rate of chain initiation at all promoters can be expected to decrease without necessary changes in the degree of repression or derepression of the genes, and thus without changes in ψ . On the other hand,

estimates of the initiation rate require fewer experimental measurements (no RNA-chain-elongation rate); their values may therefore be more accurate than the estimates of ψ . The initiation rates for rRNA and r-protein genes also respond differently to a nutritional shift-up, like ψ_r and ψ_{rp} (Table 2).

Conclusion

The non-parallel increase in the relative transcriptional activities of r-protein genes and rRNA genes (i.e. in ψ_{rp} and ψ_r , and in i_{rp} and i_r , the initiation rates at the r-protein and rRNA promoters) with increasing steady-state growth rate suggests that the synthesis rates of ribosomal components are regulated separately. This further implies that at least one of the components, and possibly both, are controlled actively and not synthesized constitutively.

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APPENDIX

Parameters Describing Gene Activities

Definitions

- G_r, G_{rp} = Number of rRNA or of r-protein genes respectively (per genome equivalent of DNA; per genome for short).
 Q = Number of chromosome origins/genome.
 $r, r_s, r_r, r_{ni}, r_{mrp}$ = Rates of synthesis of total RNA, stable RNA, rRNA, total mRNA or mRNA for r-protein respectively (nucleotides/min per genome); $r = r_s + r_m$; $r_r \approx 0.85 r_s$.
 c_s, c_r, c_m = Chain-elongation rate of stable RNA, rRNA and mRNA respectively (nucleotides/min per chain); c_r is assumed to be equal to c_s .
 M_r, M_{rp} = Molecular weight (nucleotides) of the total transcript of rRNA or r-protein genes respectively. M_r is assumed to be 5000 nucleotides = sum of 16S+23S+5S rRNA plus nucleotides lost during maturation. M_{rp} is assumed to be 21 000 nucleotides, based on a 850 000 molecular weight of all structural proteins of a 70S ribosome and 118 average mol.wt. of amino acid residues in r-protein (see the Discussion section in Dennis & Bremer, 1974a).

- t_r, t_{rp} = Transcription time (min) of rRNA or r-protein genes respectively:
 $t_r = M_r/c_r$; $t_{rp} = M_{rp}/c_m$.
 ρ = Fraction of total RNA synthesis that is stable RNA: $\rho = r_s/r$; $1 - \rho = r_m/r$.
 α_r = Differential rate of r-protein synthesis (ratio of synthesis rates, r-protein/total protein).
 N_p = Number of functioning RNA polymerase molecules/genome. N_p = number of nascent RNA chains = $(r_s/c_s) + (r_m/c_m)$.
 $\psi_s, \psi_r, \psi_m, \psi_{rp}$ = Fraction of functioning RNA polymerase engaged in the synthesis of stable RNA, rRNA, mRNA or mRNA for r-protein respectively.
 $\psi_s = \rho / [\rho + (1 - \rho)(c_s/c_m)]$ (Bremer *et al.*, 1973); $\psi_m = 1 - \psi_s$; $\psi_r \approx 0.85 \psi_s$.
 i_r, i_{rp} = Initiation rate at the rRNA and r-protein promoters respectively (RNA chains/min per promoter).

Parameters Describing Gene Activities

Gene activities may be expressed by the fraction ψ or by the initiation rate, i .

The rate of RNA-chain initiation (i , in RNA chains/min per promoter) at a given promoter is equal to the rate of synthesis (r , in nucleotides/min) of

the particular RNA divided by the molecular weight (M , in nucleotides) of the RNA species considered and by the number of genes (G) present in the sample volume considered (r and G may also be expressed in units per cell or per genome equivalent of DNA; this reference unit cancels in the quotient r/G):

$$i_r = r_r/M_r \cdot G_r = r_r/5000 G_r \quad (1)$$

$$i_{rp} = r_{rp}/M_{rp} \cdot G_{rp} = r_{rp}/21\,000 G_{rp} \quad (2)$$

The rate of rRNA synthesis (r_r) for *Escherichia coli* B/r has been measured previously (Dennis & Bremer, 1974b); the number of rRNA genes per genome (G_r) has been calculated previously under the assumption that six rRNA genes are clustered relatively close to the origin of DNA replication (Dennis & Bremer, 1973).

The rate of synthesis of mRNA for r-protein (r_{rp}) is given by

$$r_{rp} = k_r \cdot \alpha_r \cdot r_m \quad (3)$$

where k_r is a factor that corrects for the (unknown) difference in the efficiency of translation of r-protein mRNA and of average mRNA; for simplicity, we have assumed that a mRNA molecule for r-protein is translated as many times as an average mRNA molecule, i.e. $k_r = 1.0$. Since we are interested in a comparison of the initiation rates for bacteria growing in different media, the initiation rates may be normalized so that k_r cancels (Table 2, values in parentheses).

The rate of mRNA synthesis (r_m) is found from the stable-RNA synthesis rate (r_s) and the ratio of the synthesis rate for stable RNA to that for mRNA (or an equivalent ratio such as ρ = rate for stable RNA/rate for total RNA):

$$r_m = r_s[(1/\rho) - 1] \quad (4)$$

Combining eqns. (2), (3) and (4) and assuming $k_r = 1$ gives the initiation rate at the r-protein gene promoters

$$i_{rp} = \frac{r_s[(1/\rho) - 1] \cdot \alpha_r}{21\,000 G_{rp}} \quad (5)$$

The number of r-protein genes per genome (G_{rp}) is calculated from the map location of the r-protein genes on the *E. coli* chromosome (at about 64 min; Davies & Nomura, 1972). Since this is close to the origin of DNA replication (74 min; Bird *et al.*, 1972), we approximate G_{rp} by the number of origins (O) per genome, which is found from the Cooper-Helmstetter theory (Cooper & Helmstetter, 1968) of DNA replication.

We have recently reported an expression [eqn. (4) of Bremer & Dalbow (1975)] for the initiation rate at

the promoter of a gene x which contains ψ_x and the transcription time, t_x , of the gene in addition to the total number of functioning RNA polymerase molecules, N_p :

$$i_x = \frac{N_p \cdot k_x \alpha_x \psi_m}{G_x \cdot t_x} \quad (6)$$

Although it appears that this equation requires different measurements, in particular of the RNA-chain elongation rates (c_m and c_s), this equation is actually equivalent to eqns. (1) or (2). This can be shown by substituting into eqn. (6) ψ_{rp} or ψ_r respectively for $k_x \alpha_x \psi_m$, and M_{rp}/c_m or M_r/c_r respectively for t_x so that

$$i_r = \frac{N_p \cdot \psi_r \cdot c_r}{G_r \cdot M_r} \quad (7)$$

or

$$i_{rp} = \frac{N_p \psi_{rp} \cdot c_m}{G_{rp} \cdot M_{rp}} \quad (8)$$

(Note that the numerators $N_p \psi_r \cdot c_r = r_r$ and $N_p \psi_{rp} \cdot c_m = r_{rp}$.) Eqns. (7) and (8) define the relations between ψ and i .

Comparison between i and ψ , expressed in terms of measurable parameters,

$$i_r = \frac{0.85 r_s}{M_r \cdot G_r} \quad (1b)$$

$$\psi_r = \frac{0.85}{1 + [(1/\rho) - 1](c_r/c_m)} \quad (9)$$

shows that i requires knowledge of the parameters r_s , M_r and G_r , whereas ψ_r requires knowledge of the parameters ρ , c_r , and c_m . Similarly:

$$i_{rp} = \frac{0.85 \alpha_r r_s [(1/\rho) - 1]}{M_{rp} G_{rp}} \quad (5b)$$

$$\psi_{rp} = \alpha_r \left(1 - \frac{1}{1 + [(1/\rho) - 1](c_r/c_m)} \right) \quad (10)$$

Neither i_{rp} nor ψ_{rp} requires knowledge of the number of r-protein transcriptional units; i.e. if r-proteins genes have more than one promoter, then the initiation rate must be the same at each of these promoters, provided again that all r-protein mRNA species are translated with the same efficiency and that all r-proteins are made in equal numbers (Dennis, 1974).

These relationships are valid only if the turnover rates of rRNA and of r-protein are negligible, which seems to be essentially true under normal conditions of growth [see the Discussion section in Dennis & Bremer (1974b) and in Dennis (1974)].

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