Chapter 4
Part II

In prokaryotic cell
One operon = one transcript unit
Transcript unit: specific one promoter and termination site, and contain several gene
one mRNA → may translated several protein

In eukaryotic cell
Most gene expressed from separate transcription unit (discontinuous)
Transcription unit may produce several mRNA (RNA processing); one mRNA → translated only one protein
Transcription unit has two types: simple and complex

Main differences in gene structure between eukaryotes and prokaryotes

**Prokaryotes**
- No introns
- Ribosomal binding site
- Polycistronic mRNA
- No polyadenylation signal
- No 5'-capping

**Eukaryotes**
- Introns
- Exons
- Polyadenylation signal
- 5'- RNA capping (addition of methyl group to mRNA)
- No ribosomal binding site
- Monocistronic mRNA
Simple and complex eukaryotic transcription

**Simple transcription unit**

Finally, translated one protein

- Gene
- Cap site
- Exon 1
- Exon 2
- Exon 3
- Poly(A) site
- Control regions

* mRNA 5’ [ ] 3’

Mutation control region: no mRNA expression → no protein → no function

Mutation Exon: mRNA expression (some wrong) → abnormal protein → activity change

For gene that are transcribed from different promoters (regulator factor) in different cell type

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**Protein-coding genes may be solitary or belong to a gene family**

Solitary gene: in multicellular organism, 20-50% protein coding gene are represented only once in the haploid (a simple transcription unit)

Duplicated gene: gene family → protein family homologous duplicated gene encode protein with similar

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**Complex transcription units**

Multiple mRNA transcribe from primary transcript

Finally, translated more one protein

For gene that are transcribed from different promoters (regulator factor) in different cell type

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**TABLE 6-1** Major Classes of Nuclear Eukaryotic DNA and Their Representation in the Human Genome

<table>
<thead>
<tr>
<th>Class</th>
<th>L/E size</th>
<th>CPEP NUMBER IN HUMAN GENOME</th>
<th>FRACTION OF HUMAN GENOME (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Protein-coding genes</td>
<td>0.2-3500 kb</td>
<td>~25,000</td>
<td>~50% (L/E)</td>
</tr>
<tr>
<td>Tandemly repeated genes</td>
<td>≤1 kb</td>
<td>≥500</td>
<td>&lt;0.005 (L/E)</td>
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<tr>
<td>Repetitive DNA</td>
<td>≤0.5 kb</td>
<td>≤300</td>
<td>0.5</td>
</tr>
<tr>
<td>Simple-sequence DNA</td>
<td>1-500 bp</td>
<td>Variable</td>
<td>~8</td>
</tr>
<tr>
<td>LTR/retrotransposon</td>
<td>6-11 kb</td>
<td>4,000,000</td>
<td>5</td>
</tr>
<tr>
<td>Non-LTR/retrotransposon</td>
<td>100-1000 bp</td>
<td>1,000,000</td>
<td>15</td>
</tr>
<tr>
<td>Processed pseudogenes</td>
<td>Variable</td>
<td>1-1000</td>
<td>~4</td>
</tr>
<tr>
<td>Unclassified spacer DNA</td>
<td>Variable</td>
<td>n.a.</td>
<td>~25</td>
</tr>
</tbody>
</table>

* Complete transcription units including introns.
* Transcription units not including introns. Protein-coding regions total 1.7% of the genome.
* Length of tandemly repeated sequences.
* Frequencies between transcription units that are not repeated in the genome; n.a. = not applicable.
New Roles of RNA

RNAi - RNA interference
siRNA - active molecules in RNA interference; degrades mRNA (act where they originate)
miRNAs - tiny 21–24-nucleotide RNAs; probably acting as translational regulators of protein-coding mRNAs

stRNA - Small temporal RNA; (ex. lin-4 and let-7 in Caenorhabditis elegans)
snRNA - Small nuclear RNA; includes spliceosomal RNAs (processing)
snoRNA - Small nucleolar RNA; most known snoRNAs are involved in rRNA modification

Alternative RNA splicing increases the number or proteins expressed from a single eukaryotic gene

Higher eukaryote have multidomain tertiary structure only from a small number of exons.
Single gene → Multiple introns → alternative splicing → protein isoforms
Alternative splicing: The presence of multiple introns in many eukaryotic genes permits expression of multiple, related proteins form a single gene.
> 20 isoforms fibronectin from different alternatively spliced mRNA

Cell type specific splicing of fibronectin pre-mRNA
Differences Between Transcription In Prokaryotes and Eukaryotes

Transcription And Translation In Prokaryote--------the same time
Eukaryotic Transcription and translation-------------different time
Processing Eukaryotic mRNA

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Simple and complex eukaryotic transcription

Simple transcription unit

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Mutation Exon: mRNA expression (some wrong) → abnormal protein → activity change

Different cell different transcription
Transcriptional control of gene expression

Key players
1. Promoter
2. RNA polymerase
3. Transcription factor (regulator)
4. Operator (or enhancer)

In prokaryotic cell
In eukaryotic cell: DNA high condense → need decondense → open

Control of gene expression in prokaryotes
Repressed: the corresponding mRNA and encoded protein are synthesis at low rates
Activated: at high rates
Operator: in DNA, might have activated and repressed. Determined by activator and repressor (a DNA binding protein)
Highly regulated in order to adjust the cell’s enzymatic machinery and structural components to changes in the nutritional and physical environment.
The lac operon in E. coli as primary example.
Operon is transcribed from one start site into a single mRNA, all the genes within an operon are coordinately regulated.

Repressors - which inhibit transcription by binding to an ‘operator’ DNA sequence near the promoter
- which can be modulated by
  - Effectors
  - Co-repressors

Activators - which enhance transcription by binding a DNA sequence near the promoter sequence
- these may or may not be modulated by an effector
Transcription initiation by bacterial RNA polymerase requires association with a sigma factor

Operons: each of encodes enzymes gene involved in a particular metabolic pathway or protein
All the gene are coordinately regulated: that is they are all activated or repressed (要就全部表現, 不然全部不表現)
Initiate stage: RNA polymerase bind sigma factor (σ70) → σ 70 recognize to promoter sequence (6 base pair) about -10 → - 10 to -35 is promoter region →RNA polymerase plus σ70 bind it (RNA π is bind to -50 to 20)→ interact with DNA double strand → σ 70 is initiation factor

Initiation of lac operon transcription can be repressed and activated
σ70 subunit of RNA polymerase bind to the lac promoter, it upstream of the start site.
When no lactose (or low concentration), lac repressor bind to operator, which overlaps the transcription start site → block polymerase bind
When lactose increase → lactose bind to lac repressor → lac repressor conformation change → lac repressor can not bind operator → transcription start exposure → polymerase bind → transcription easy
Glucose overuse → cAMP ↑ → bind to CAP protein → conformation change → interaction with polymerase → transcription ↑

Catabolite Activator Protein (CAP)

Schematics of (a) positive regulation of gene transcription and (b) negative regulation of gene transcription

Lac repressor-operator interactions

Strong promoter: a high rate
Weak promoter: a low rate
RNA polymerase (RNAP) vs. Transcription

Three eukaryotic polymerases catalyze formation of different RNAs

<table>
<thead>
<tr>
<th>POLYMERASE</th>
<th>RNA TRANSCRIBED</th>
<th>RNA FUNCTION</th>
</tr>
</thead>
<tbody>
<tr>
<td>RNA polymerase I</td>
<td>Pre-rRNA (28S, 18S, 5.8S) RNAs</td>
<td>Ribosomes component, protein synthesis</td>
</tr>
<tr>
<td>RNA polymerase II</td>
<td>mRNA, snRNA, miRNA</td>
<td>Encodes protein</td>
</tr>
<tr>
<td></td>
<td></td>
<td>RNA Splicing, Post-transcriptional gene control</td>
</tr>
<tr>
<td>RNA polymerase III</td>
<td>tRNAs, 5S rRNA, 5.8S rRNA, 7S rRNA</td>
<td>Protein synthesis</td>
</tr>
<tr>
<td></td>
<td>Other stable short RNAs</td>
<td>RNA Splicing, Signal recognition particle for insertion of polyproteins into the endoplasmic reticulum, Various functions, unknown for many</td>
</tr>
</tbody>
</table>

- α-amanitin from *Amanita Phalloides* binds tightly to RNA Pol II and blocks transcriptional elongation.
- RNA Pol I transcribe 1 gene at ~200 copies. The gene for the 45S pre-rRNA is present in tandem array.
- RNA Pol II transcribe ~25,000 genes;
- RNA Pol III transcribe 30-50 genes at variable copy numbers.

DNA affinity chromatography for purification

α-amanitin在很低的濃度即可抑制RNA pol II活性
Similar, but Yeast RNAPII more complex than bacterial CTD; carboxyl-terminal domain

Comparison of 3-D structures of bacterial and eukaryotic RNA polymerases

(a) Bacterial RNA polymerase (b) Yeast RNA polymerase II (c) Yeast RNA polymerase II

CTD; carboxyl-terminal domain

Try-Ser-Pro-Thr-Ser-Pro-Ser: CTD, repeat sequence. Phosphorylation → RNAP II → initiate transcript

Schematic representation of the subunit structure of E. Coli RNA core polymerase and yeast nuclear RNA polymerase

All three yeast polymerases have five core subunits that exhibit some homology with the β, β' α and ω subunits in E. coli RNA polymerase. RNA polymerases I and III contain the same two non-identical α-like subunits, whereas polymerase II has two copies of a different α-like subunit. All three polymerases share four other common subunits. In addition, each RNA polymerase contains three to seven unique smaller subunits. The largest subunit (1) of RNA polymerase II also contains an essential C-terminal domain (CTD). 27 (yeast) to 52 (human) copies of (YSPTSPS). Phosphorylation of CTD is important for transcription and RNA processing.

Puffed region

The region of geomes is very actively transcribed.

Antibody staining demonstrates that the CTD of RNAP II is phosphorylated during in vivo transcription.

Green: unphosphorylated
Red: phosphorylated

RNAP HOLOENZYME - σ70
Promoter-specific transcription initiation

In the Holoenzyme:

· β' binds DNA
· β binds NTPs
· β and β' together make up the active site
· α subunits appear to be essential for assembly and for activation of enzyme by regulatory proteins. They also bind DNA.
· σ recognizes promoter sequences on DNA
**The assembly pathway of the core enzyme**

\[
\alpha \rightarrow \alpha_2 \rightarrow \alpha_2\beta \rightarrow \alpha_2\beta\beta' = \text{core enzyme}
\]

**CORE ENZYME**
Sequence-independent, nonspecific transcription initiation

**SIGMA SUBUNIT**
Interchangeable, promoter recognition

- \(\sigma^{70}\)
- \(\sigma^{32}\)
- \(\sigma^{60}\)

- Vegetative (principal \(\sigma\))
- Heat shock (for emergencies)
- Nitrogen starvation (for emergencies)

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**RNA polymerase II initiates transcription at DNA sequence corresponding to the 5’ cap of mRNA**

Need 5’ cap for efficient translation

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**Proteins associate into multimeric structures and macromolecular assemblies**

The mRNA transcription-initiation machinery

1. DNA
2. RNA polymerase
3. Mediator complex
4. Transcription preinitiation complex
**TBP (TATA-box binding protein)**

- Conserved C-terminal domain of 180 amino acids.
- A monomer with a saddle-shaped structure; the two halves show an overall dyad symmetry but are not identical.
- Binds multiple transcription factors (TAFs, TFIIB, and TFIIA).
- Binds in the minor groove and significantly bends DNA.

**TFIID** — consists of TBP (TATA-box binding protein) + TAFs (TBP-associated factors). Binds to core promoter motifs. TAFs interact with activator proteins. The first step in basal transcription is probably binding of TFIID to the core promoter.

**TFIIB** — one subunit of 35 kDa. Binds to TBP and the BRE.

**RNA Polymerase II** — consists of two large subunits (Ila and Iib) as well as about eight smaller subunits. Unique feature of largest (Ila) subunit is the C-terminal domain (CTD), which is an imperfectly-repeated heptad repeat motif, YSPTSPS.

**TFIE** — also known as RAPE274. Binds to RNA polymerase II. Two subunits of 30 and 74 kDa. Functions in transcription initiation and elongation.

**TFIIH** — two polypeptides of 34 and 56 kDa. Required for assembly of TFIIH into the transcription preinitiation complex (PIC).

**TFIH** — nine polypeptides. Core TFIIH has six subunits, which include 5′→3′ and 3′→5′ DNA helicases, and is also involved in nucleotide excision repair. Also has a three subunit Cdk7/Mo15 + Cyclin H + MAT1 kinase complex that phosphorylates Ser5 of the CTD during transcription initiation.
Model for the structure of and RNAP II preinitiation complex

In vivo transcription initiation by RNAP II requires additional proteins

TFIIH mutation

色素性乾皮病 xeroderma pigmentosum

皮肤和覆盖眼睛的组织对紫外线部分极其敏感；类似癌症

柯凱因氏症候群 Cockayne syndrome

Positive and Negative Regulation in the lac Operon

Operon has three structural genes: lacZ, lacY, lacA

lacI gene is upstream and in the opposite orientation (方向)

Catabolite Activator Protein (CAP) is a positive regulatory protein and cyclic AMP is its inducer molecule.

Lac Repressor (lacI) gene is a negative regulatory protein, and lactose (or IPTG) is its inducer molecule.

Lac repressor as Tetramer binds two regions of the DNA

Forms a loop of DNA between the two binding sites

Binding prevents transcription

Allosteric enzyme with binding site for allo-lactose affecting one dimer of the tetramer
The lac operon is also subject to POSITIVE regulation, by CAP in the presence of cAMP. 

The lac operon is induced by the presence of lactose in the medium, but *E. coli* prefers to use glucose (better energy source). 

→ lac operon is also regulated by glucose levels 
  [glucose] = high → Low transcription of lac operon 
  [glucose] = low → High transcription of lac operon 

This correlates to the activity of CAP which activates lac operon in the presence of cAMP (cyclic AMP) 

[glucose] = low → [cAMP] = high 
[glucose] = high → [cAMP] = low 

Levels of Control of Lac Operon Expression

3 Scenarios 情節：

1) No Lactose around 
   • Operon switched off, essentially no mRNA regardless of [glucose] 

2) Lactose present; glucose also present 
   • The presence of lactose inactivates the repressor 
     → low level of transcription occurs 
   • Glucose present → cAMP is low → CAP does not ‘help’ transcription and thus it remains at low level 

3) Lactose present; no glucose 
   • The presence of lactose inactivates the repressor 
   → Transcription occurs 
   • NO Glucose → cAMP is high → cAMP binds CAP (becomes activated) 
   → CRP binds & ‘Helps’ Transcription 
   • High Level of transcription 

Lac operon flash 

Small molecules regulate expression of many prokaryotic gene via DNA-binding repressor 

Specific repressor binds to operator → blocking transcription initiation 
Small molecules, called inducer, binds to repressor → controlling DNA-binding activity and transcription rates 

For example: 
Tryptophan: when trp high → bind to trp repressor → conformational change → repressor easy bind to operator → transcription low 
lac operon: inducer lactose; lactose bind to lac repressor → conformational change → bind to operator hard → transcription high 

Transcription by σ^{54} RNA polymerase is controlled by activator that bind far from the promoter 

σ^{70} is major form of the bacterial enzyme. 
Transcription of certain groups of genes, is carried out by RNA polymerases containing one of several alternative sigma factors the recognized different consensus promoter sequences than σ^{70}. 
σ^{54} is also one of RNA polymerase subunit, is regulated solely (唯—) by activators whose binding sites in DNA. Referred to as enhancer, it can activate transcription. 
For example: 
NtrC (nitrogen regulatory protein C)-stimulates transcription from the promoter of the glnA gene (encodes glutamine synthetase) 

Autokinase Sensor Proteins (NtrB) (autophosphorylation) 
  – Sensor domain 
  – Transmitter domain (C-terminus) 
Response Regulators (NtrC) 
  – N-terminal receiver domain 
  – Cross-regulation 

Phosphorylation: 在蛋白質 ser, tyr, thr的位置接上磷酸根
σ54 binds to the glnA promoter (did not melt DNA and transcription) → bind with NtrC and enhancer → turn on glnA → glutamine synthetase mRNA → transcription ↑

Normal condition: glutamine ok

Pair of phosphorylated NtrC dimers α54 – RNA polymerase

NtrC dimers α54 – RNA polymerase

Low glutamine:
NtrB phosphorylates NtrC → NtrC conformational change → binds to enhancer upstream of the glnA promoter.
NtrC and NtrB are regulatory protein for transcription.

Experimental evidence for population shift
Nitrogen Regulatory Protein C (NtrC) plays a central role in the bacterial metabolism of nitrogen

N-terminal receiver domain
DNA binding domain
Central catalytic domain

Nitrogen Regulatory Protein C (NtrC) plays a central role in the bacterial metabolism of nitrogen
Changing nitrogen levels promote the activity of NtrB kinase.

NtrB kinase phosphorylates NtrC at aspartate 54 in the receiver domain.

Protein conformational change

Phosphorylation promotes conformational change in the receiver domain.

Protein conformational change

• NtrC – active and inactive conformations apparent
• P-NtrC – protein shifted towards activated conformation

Many bacterial responses are controlled by two-component regulatory system (NtrB, NtrC and PhoR, PhoB).

Low phosphate in the environment and periplasmic space.

When external environment phosphate ↓→ periplasmic space phosphate ↓→ PhoR can not bind phosphate → Conformational change and dissociate → kinase domain exposure → transfer ATP phosphate → to Pho B → transcription

The second protein also called a response regulator. One PhoR can phosphorylated many PhoB.
The three roles of RNA in protein synthesis

1. **Information carrier**: mRNA
2. **Adaptor molecule**: tRNA
3. **Catalyst and structural molecule**: rRNA

### Transfer RNA (tRNA)

All types of RNA, including tRNA, are transcribed from template DNA.

- tRNA is a single-stranded RNA only about 80 nucleotides.
- 45 distinct types of tRNA, some tRNAs recognize two or more mRNA codons specifying the same AAs.
- The enzymes that catalyze the attachment of an AA to its tRNA are specific to each AA.

### Ribosomal RNA (rRNA)

Ribosomes coordinate the pairing of tRNA anti-codons to mRNA codons.

- Two subunits (small and large)
- 60% rRNA and 40% protein
- Both subunits are constructed in the nucleolus; once in the cytoplasm, are assembled into functional ribosomes when attached to an mRNA.

### Messenger RNA (mRNA)

Carries the genetic information transcribed from DNA in the form of a series of three nucleotide sequences, called codons, each of which specifies a particular amino acid.

- Of the 64 possible codons in the genetic code, 61 specify individual amino acids and three are stop codons.

### Reading frame

The sequence of codons that runs from a specific start codon to a stop codon.
Start codon: most is AUG start (initiator) codon-methionine in eukaryote.
Stop codon: UAA, UGA, UAG
Reading frame: the sequence of codons that runs from a specific start codon to a stop codon. In eukaryote, exon = reading frame

Folded structure of tRNA promotes decoding (解譯) functions
DNA (4 nucleotide) → mRNA → protein (20 types), need tRNA and aminoacyl-tRNA synthetase (very specific)
enzymes that catalyzes the attachment of an AA to its tRNA Each of the 20 AAs has a specific aminoaeryl-tRNA synthetase
30-40 different tRNAs in bacterial, 50-100 in animal and plant, it more than the number of amino acids (20); many amino acid have more than one tRNA; many tRNA pair with more codons

The structure of tRNA
1. About 70-80 nucleotide long
2. The exact nucleotide sequence varies among tRNA. All tRNA fold into a similar stem-loop arrangement in 2 dimensions (four base-pair stems and three loops), like cloverleaf (苜蓿)
3. The four stems are short double helices stabilized by Watson-Crick base pairing
4. The loops about 7-8 nucleotides
5. The CCA sequence at the 3’ end is found in all tRNAs
6. Attachment of amino acid to the 3’ end
7. Some A,U,C,G are modified and located in specific region
Wobble Hypothesis (position)

Each codon is the same in most known organisms
But some exceptions to the general code probably were later evolutionary developments

<table>
<thead>
<tr>
<th>CODON</th>
<th>UNIVERSAL CODE</th>
<th>UNIVERAL CODE*</th>
<th>OCCURRENCE</th>
</tr>
</thead>
<tbody>
<tr>
<td>UGA</td>
<td>Stop</td>
<td>Top</td>
<td>Mycoplasma, Spinifex, mito-</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>chondria of many species</td>
</tr>
<tr>
<td>CGG</td>
<td>Leu</td>
<td>Thr</td>
<td>Mitochondria in yeast</td>
</tr>
<tr>
<td>UAA, UAG</td>
<td>Stop</td>
<td>Gln</td>
<td>Actinobacteria, Tetradinera,</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Pancreas, etc.</td>
</tr>
<tr>
<td>UGA</td>
<td>Stop</td>
<td>Cys</td>
<td>Raguaria</td>
</tr>
</tbody>
</table>

*Found in nuclear genes of the listed organisms and in mitochondrial genes as indicated. From T. Ohara et al., 1992, Mitochondr. Dev. 3(2):29.

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Wobble Hypothesis (position)
3D structures of RNA: transfer-RNA structures

- Secondary structure of tRNA (cloverleaf)
- Tertiary structure of tRNA

The “cloverleaf” model of tRNA emphasizes the two major types of secondary structure, stems & loops. tRNAs typically include many modified bases, particularly in loop domains.

tRNA

RNA structure:
Most RNA molecules have secondary structure, consisting of stem & loop domains.

- Double helical stem domains arise from base pairing between complementary stretches of bases within the same strand. These stem structures are stabilized by stacking interactions as well as base pairing, as in DNA.
- Loop domains occur where lack of complementarity or the presence of modified bases prevents base pairing.

There are 61 codons specifying 20 amino acids. Minimally 31 tRNAs are required for translation, not counting the tRNA that codes for chain initiation. Mammalian cells produce more than 150 tRNAs.
Nonstandard base pairing often occurs between codons and anticodons

In perfect condition, codons and anticodons cells would have to contain exactly 61 different tRNA species. Codons and anticodons might specific recognize However, most cell contain fewer than 61 tRNA. So broad recognition can occur.

Wobble position: broader recognition of nonstandard pairing between bases. The third of 3’ end base in mRNA and corresponding first base in its tRNA.

The first and second base of codon (mRNA) almost formed standard base pair.
adrenaline deaminated → inosine (I) → form nonstandard base pairs.

I similar to G, A

In 1965, Holley determined the sequence of yeast tRNA(ala): he found the nucleotide Inosine at the 5’ end in the anticodon.

Wobble hypothesis (Crick, 1966)

Inosine Uracil

adenine deaminated → inosine (I) → form nonstandard base pairs.
I = inosine which is sometimes found in tRNA
The Wobble Hypothesis
A tRNA can frequently recognize several codons because of non standard Watson-Crick hydrogen bonding between the nucleotides.
This effect is called the **wobble hypothesis**.
The first two bases of the codon make normal (canonical) H-bond pairs with the 2nd and 3rd bases of the anticodon.
At the remaining position, less stringent rules apply and noncanonical pairing may occur.
The rules: first base U can recognize A or G, first base G can recognize U or C, and first base I can recognize U, C or A (I comes from deamination of A).
Advantage of wobble: dissociation of tRNA from mRNA is faster and protein synthesis also.

**Aminoacyl-tRNA Synthetases** catalyze linkage of the appropriate amino acid to each tRNA.
The reaction occurs in 2 steps.
In step 1, an O atom of the amino acid α-carboxyl attacks the P atom of the initial phosphate of ATP.

**Aminoacyl-tRNA Synthetase** - summary:
1. amino acid + ATP \rightarrow aminoacyl-AMP + PP_i
2. aminoacyl-AMP + tRNA \rightarrow aminoacyl-tRNA + AMP

The 2-step reaction is **spontaneous** overall, because the concentration of PP_i is kept low by its hydrolysis, catalyzed by Pyrophosphatase.
Activate amino acids by covalently linking them to tRNAs.
Ribosomes are protein-synthesizing machines. Increase synthesis of protein about 2-5 aa/sec.

<table>
<thead>
<tr>
<th>Subunits</th>
<th>Proteins</th>
<th>rRNA</th>
</tr>
</thead>
<tbody>
<tr>
<td>3 subunits</td>
<td>+ Total: 21</td>
<td>16S</td>
</tr>
<tr>
<td>4 subunits</td>
<td>+ Total: 33</td>
<td>16S</td>
</tr>
</tbody>
</table>

S: svedberg units, a measure of the sedimentation rate of suspended particles centrifuged under standard conditions.

**Ribosome Composition (S = sedimentation coefficient)**

<table>
<thead>
<tr>
<th>Ribosome Source</th>
<th>Whole Ribosome</th>
<th>Small Subunit</th>
<th>Large Subunit</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. coli</td>
<td>70S</td>
<td>30S</td>
<td>50S</td>
</tr>
<tr>
<td></td>
<td>16S RNA</td>
<td>21 proteins</td>
<td>23S &amp; 5S RNAs</td>
</tr>
<tr>
<td>Rat cytoplasm</td>
<td>80S</td>
<td>40S</td>
<td>60S</td>
</tr>
<tr>
<td></td>
<td>18S RNA</td>
<td>33 proteins</td>
<td>28S, 5.8S, &amp;5S RNAs</td>
</tr>
</tbody>
</table>

Eukaryotic cytoplasmic ribosomes are larger and more complex than prokaryotic ribosomes. Mitochondrial and chloroplast ribosomes differ from both examples shown.

Ribosomal RNA (rRNA) associates with a set of proteins to form ribosomes, structures that function as protein-synthesizing machines.

**Ribosomes**

<table>
<thead>
<tr>
<th>Origin</th>
<th>Complete ribosome</th>
<th>Ribosomal subunit</th>
<th>rRNA components</th>
<th>Proteins</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cytosol</td>
<td>80 S</td>
<td>40 S</td>
<td>18 S</td>
<td>C.30</td>
</tr>
<tr>
<td></td>
<td></td>
<td>60 S</td>
<td>5 S</td>
<td>C.50</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>5.8 S</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>25 S</td>
<td></td>
</tr>
<tr>
<td>Chloroplasts</td>
<td>70 S</td>
<td>30 S</td>
<td>16 S</td>
<td>C. 24</td>
</tr>
<tr>
<td></td>
<td></td>
<td>50 S</td>
<td>4.5 S</td>
<td>C. 35</td>
</tr>
<tr>
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<td></td>
<td></td>
<td>5 S</td>
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<td></td>
<td>23 S</td>
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<td>Mitochondrion</td>
<td>78 S</td>
<td>~ 30 S</td>
<td>18 S</td>
<td>C. 33</td>
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<td></td>
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<td>~ 50 S</td>
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<td>26 S</td>
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Structure of E. Coli 70S ribosome as determined by x-ray crystallography.

23S rRNA + protein

16S rRNA + protein

Structure (E. coli) 70S ribosome as determined by x-ray crystallography.