Transcription & Translation

Lecture 28 (12/1/25)

- **Transcription**
    - Overview-mRNA structure
    - Process
    - RNA Polymerase
    - Fidelity ⇐
- **Translation**
    - Genetic Code
        - triplet
        - deciphering
    - tRNA
        - Structure
        - Anticodon
        - Acylation (charging)
            - Aminoacyl-tRNA Synthetases
            - Mechanism
            - Fidelity ⇐
    - Protein Biosynthesis
        - Overview
        - Process
        - Ribosome review
        - Elongation
            - Decoding: Fidelity ⇐
            - Peptidyl Transferase
        - Energy

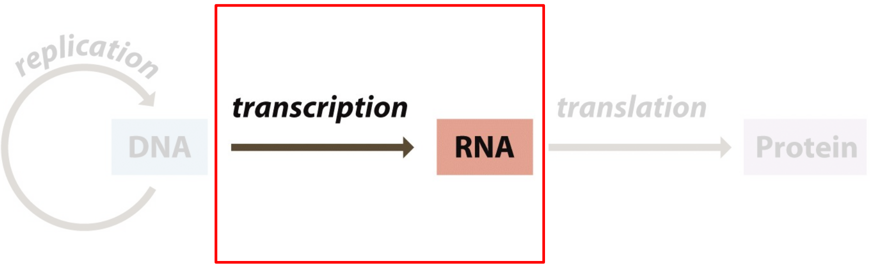
TODAY
- Reading: Ch26, 960-964; Ch27, 1006-1013, 1018-1024, 1015-1018, 1028-1036

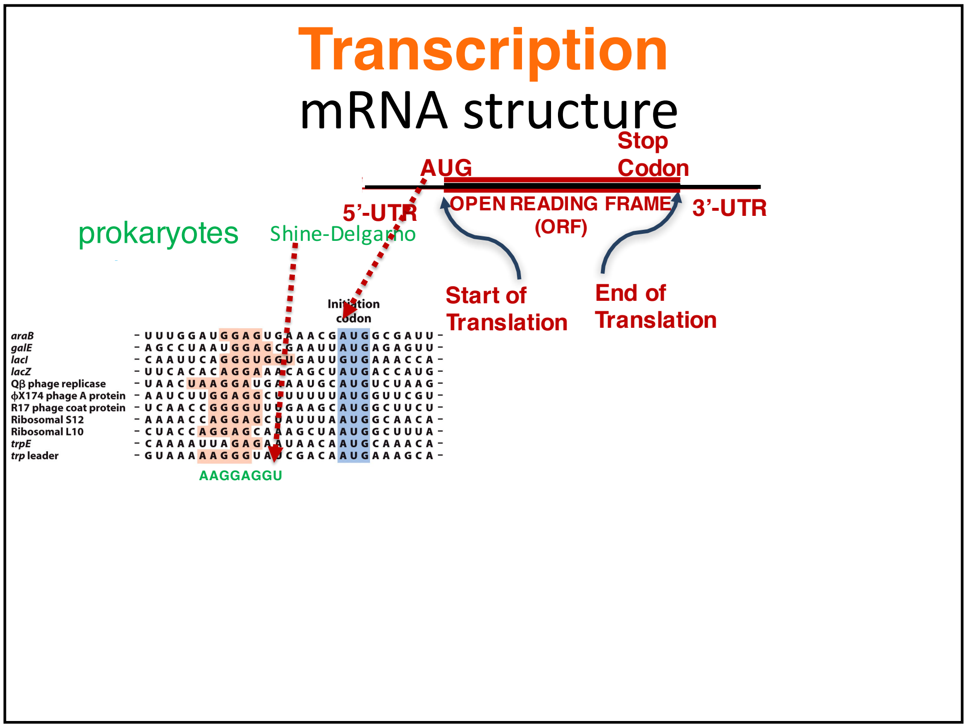
Homework: #28, #29, #30

NEXT
- Reading: Ch10; 341-348
- Homework: #31

Transcription

Nucleic acid function: Central Dogma





Transcription

mRNA structure

AUG

Stop Codon

5’-UTR

OPEN READING FRAME (ORF)

3’-UTR

Start of Translation

End of Translation

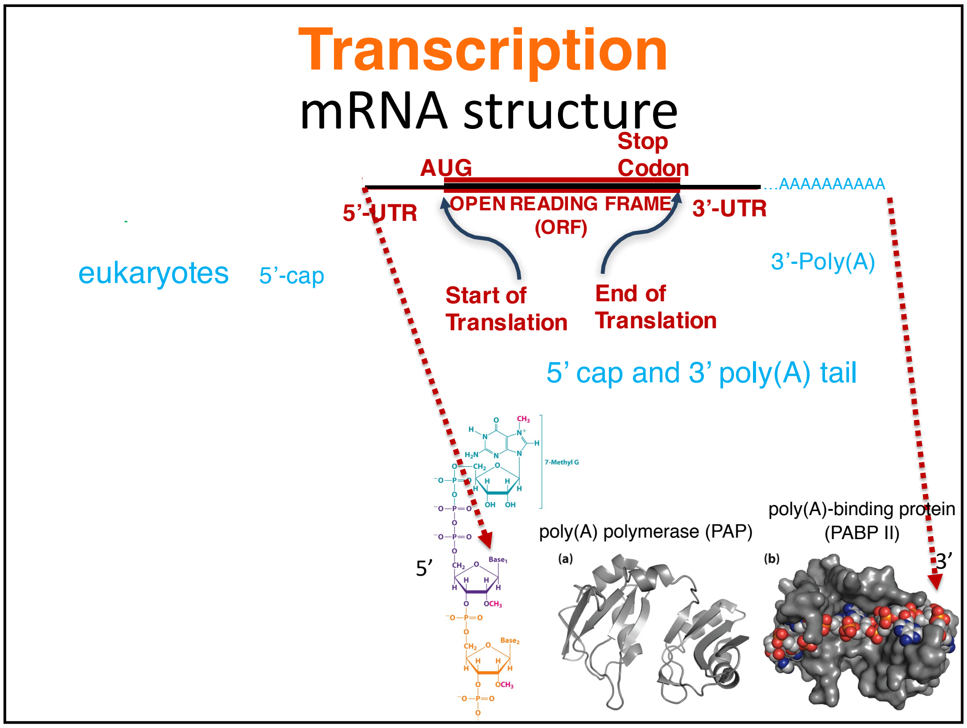
prokaryotes

Shine-Delgarno

Initiation codon

araB	- U U U G G A U G G A G U G A A A C G A U G G C G A U U -
galE	- A G C C U A A U G G A G C G A A U U A U G A G A G U U -
lacI	- C A A U U C A G G G U G G U G A U U G U G A A A C C A -
lacZ	- U U C A C A C A G G A A A C A G C U A U G A C C A U G -
Qβ phage replicase	- U A A C U A A G G A U G A A A U G C A U G U C U A A G -
ϕX174 phage A protein	- A A U C U U G G A G G C U U U U U U A U G G U U C G U -
R17 phage coat protein	- U C A A C C G G G G U U U G A A G C A U G G C U U C U -
Ribosomal S12	- A A A A C C A G G A G C U A U U U A A U G G C A A C A -
Ribosomal L10	- C U A C C A G G A G C A A A G C U A A U G G C U U U A -
trpE	- C A A A A U U A G A G A A U A A C A A U G C A A A C A -
trp leader	- G U A A A A A G G G U A U C G A C A A U G A A A G C A -

AAGGAGGU



Transcription

mRNA structure

AUG

Stop Codon

…AAAAAAAAAA

5’-UTR

OPEN READING FRAME (ORF)

3’-UTR

eukaryotes

5’-cap

Start of Translation

End of Translation

3’-Poly(A)

5’ cap and 3’ poly(A) tail

poly(A) polymerase (PAP)

poly(A)-binding protein (PABP II)

Transcription

Process:

- **Initiation**
- **Elongation**
- **Termination**

RNA Polymerases need 3 things:

- NTPs
- Template
- Place to start (NO primer needed)

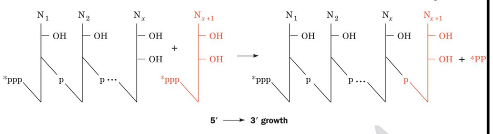
$$(\text{RNA})_{n\text{ residues}} + \text{NTP} \xrightleftharpoons[\text{RNA Polymerase}]{} (\text{RNA})_{n+1\text{ residues}} + \text{PP}_i \xrightarrow[\text{pyrophosphatase}]{\text{H}_2\text{O}} 2\,\text{P}_i$$

(5′) CGCTATAGCGTTT (3′) DNA nontemplate (coding) strand (aka: sense, Crick)

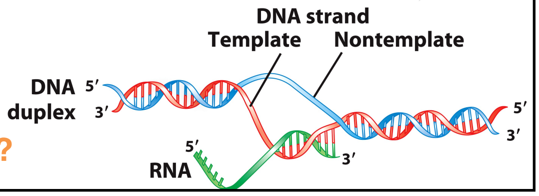
(3′) GCGATATCGCAAA (5′) DNA template strand (aka: anti-sense, Watson)

What is the sequence of the newly synthesized RNA strand?

5'-CGCUAUAGCGUUU-3'



Direction of transcription



What about a place to start?

Promoters

Transcription

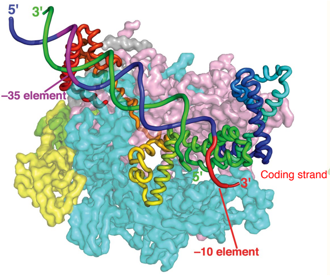
Prokaryotic Transcription – Initiation (a place to start)

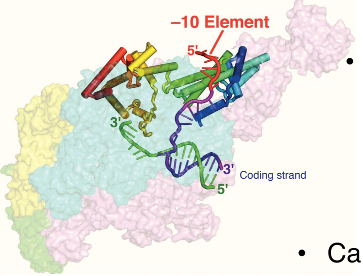
Operon	−35 region … −10 region (Pribnow box) … Initiation site (+1)
lac	ACCCCAGGCTTTACACTTTATGCTTCCGGCTCGTATGTTGTGTGGAATTGTGAGCGG
lacI	CCATCGAATGGCGCAAAACCTTTCGCGGTATGGCATGATAGCGCCCGGAAGAGAGTC
galP2	ATTTATTCCATGTCACACTTTTCGCATCTTTGTTATGCTATGGTTATTTCATACCAT
araBAD	GGATCCTACCTGACGCTTTTTATCGCAACTCTCTACTGTTTCTCCATACCCGTTTTT
araC	GCCGTGATTATAGACACTTTTGTTACGCGTTTTTGTCATGGCTTTGGTCCCGCTTTG
trp	AAATGAGCTGTTGACAATTAATCATCGAACTAGTTAACTAGTACGCAAGTTCACGTA
bioA	TTCCAAAACGTGTTTTTTGTTGTTAATTCGGTGTAGACTTGTAAACCTAAATCTTTT
bioB	CATAATCGACTTGTAAACCAAATTGAAAAGATTTAGGTTTACAAGTCTACACCGAAT
*t*RNA$^{\text{Tyr}}$	CAACGTAACACTTTACAGCGGCGCGTCATTTGATATGATGCGCCCCGCTTCCCGATA
rrnD1	CAAAAAAATACTTGTGCAAAAAATTGGGATCCCTATAATGCGCCTCCGTTGAGACGA
rrnE1	CAATTTTTCTATTGCGGCCTGCGGAGAACTCCCTATAATGCGCCTCCATCGACACGG
rrnA1	AAAATAAATGCTTGACTCTGTAGCGGGAAGGCGTATTATGCACACCCCGCGCCGCTG

Consensus sequence: (Coding strand)

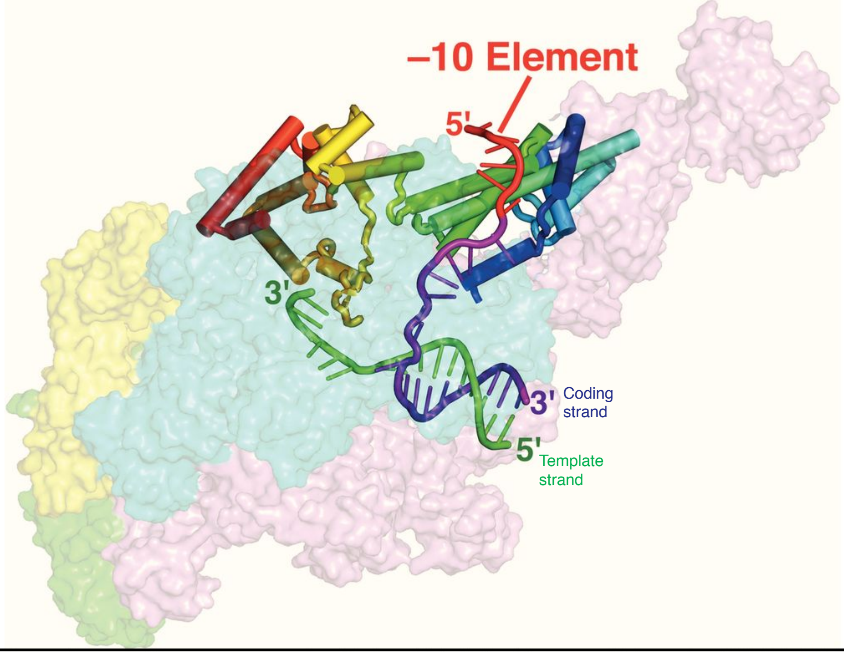
	−35 region		−10 region		Initiation site
	T T G A C A	… 16–19 bp …	T A T A A T	… 5–8 bp …	A 51 C 55 T 48 G 42
	69 79 61 56 54 54		77 76 60 61 56 82		

- RNA pol requires signal to begin transcription
  - ***why?***
- σ factor recognizes **promoter** region of a gene/operon (–10 & –35 regions)
  - σ factor-RNA polmerase complex work together to transcribe DNA at specific start sites.
  - Once σ factor interacts with –10 element, the complex unwinds DNA ~2 turns (open complex).
- Called the "Holoenzyme"



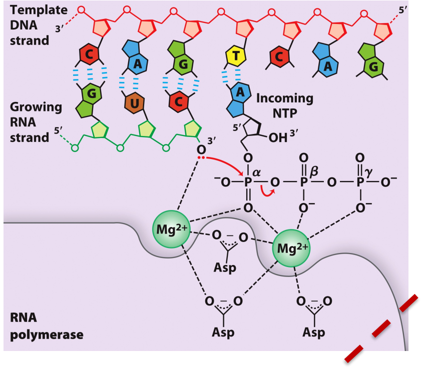


RNAP Complexed With Promoter

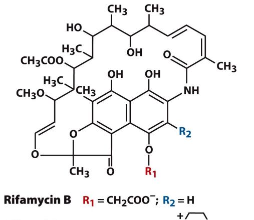


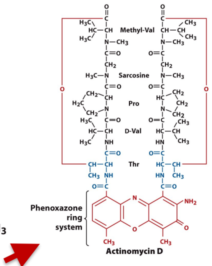
Transcription

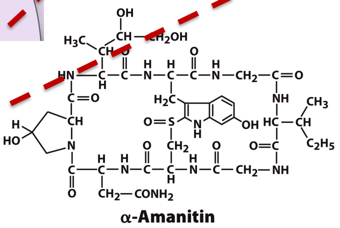
Mechanism

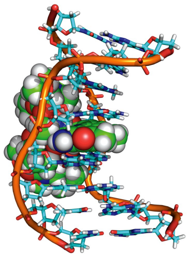


Inhibitors of Transcription









Actinomycin D-DNA complex
PDBid 1DSC

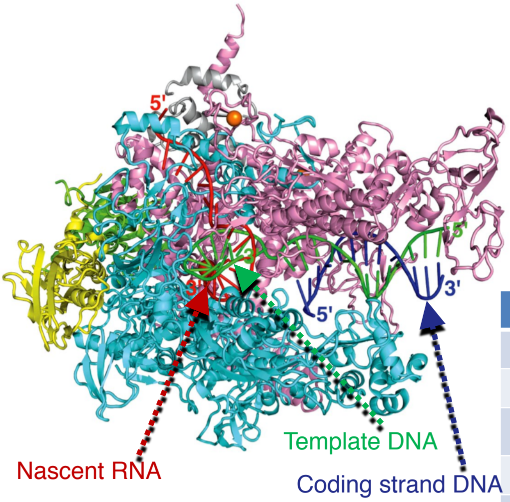
Inhibits elongation at first phosphodiester bond

Inhibits elongation by intercalating

Inhibits EUKARYOTIC RNAPs (only I & III)

Transcription

RNA Polymerase Structure



RNA pol is a multi-subunit enzyme ($\alpha_2\beta\beta'\omega\sigma$)

These subunits make up the **core complex:**

- two **α** subunits make non-specific contacts with DNA for positioning
- the **β** and **β'** subunits catalyze the addition of ribonucleotides to the growing chain
- the **ω** subunit acts to stabilize the complex

Subunit	Gene	MW	#	Role
α_2	*rpoA*	34	2	Non-specific DNA binding
β	*rpoB*	150	1	Polymerase
β'	*rpoC*	155	1	Non-specific DNA binding & polymerase
ω	*rpoZ*	10	1	Zn^{2+} binding
σ	*rpoD*	70	1	Promoter recognition

RNA•DNA duplex is in the A-form
It uses the same mechanism for correct W-C bp and fidelity
Therefore, error rate is the same 1/10,000

Rate is ~ 50 base/sec
Processivity is ~2000 bp

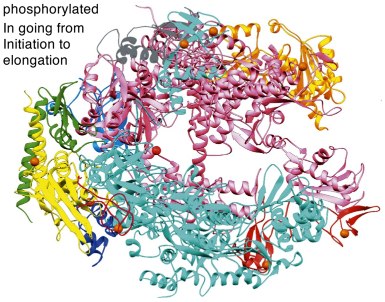
No 3'→5' exonuclease proofreading

Transcription

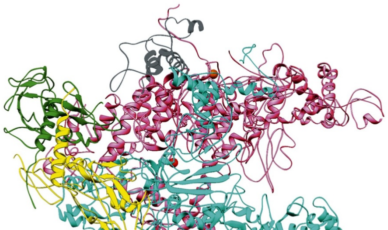
Eukaryotic RNA Polymerase II Conformations

Also, the β' homolog has a disordered CTD that is phosphorylated

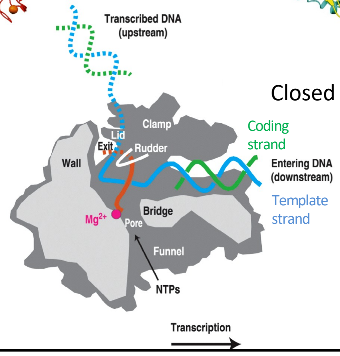
In going from Initiation to elongation



Open conformation



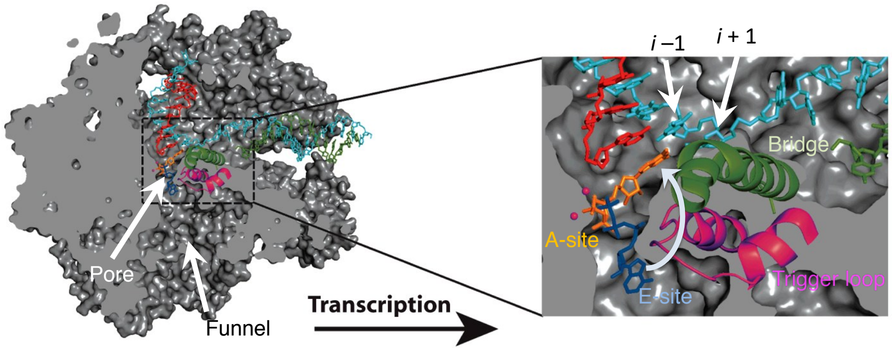
Closed conformation



Yeast RNA polymerase
PDBid 1I50

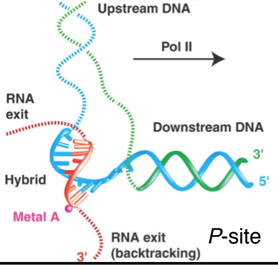
Transcription

Eukaryotic RNA Polymerase II NTP sites (A & E)



Backtracking

RNAP is very sensitive to the helix shape in the active site. If there is a mispaired nucleotide, or even a deoxy nucleotide, it stalls (as well as at damaged DNA).
The helix unwinds and the 3'-end of the RNA goes into a *P*-site.
Other subunits/proteins hydrolyze RNA at 3'-end.



Proofreading

RNA polymerase II
PDBid 2E2H

Transcription & Translation

Transcription
- Overview
- Process
- RNA Polymerase
- Fidelity

Translation
- Genetic Code
  - triplet
  - deciphering
- tRNA
  - Structure
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    - Peptidyl Transferase
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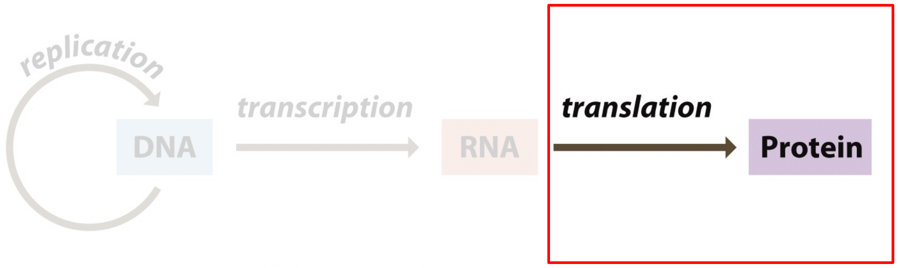
Transcription & Translation

Nucleic acid function: Central Dogma


replication

DNA

transcription

RNA

translation

Protein

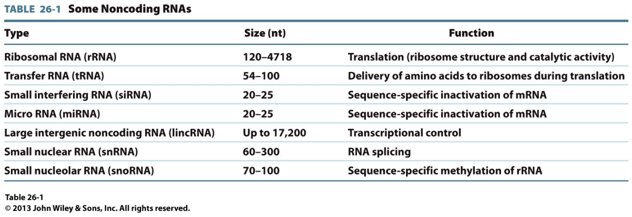


TABLE 26-1 **Some Noncoding RNAs**

Type	Size (nt)	Function
Ribosomal RNA (rRNA)	120–4718	Translation (ribosome structure and catalytic activity)
Transfer RNA (tRNA)	54–100	Delivery of amino acids to ribosomes during translation
Small interfering RNA (siRNA)	20–25	Sequence-specific inactivation of mRNA
Micro RNA (miRNA)	20–25	Sequence-specific inactivation of mRNA
Large intergenic noncoding RNA (lincRNA)	Up to 17,200	Transcriptional control
Small nuclear RNA (snRNA)	60–300	RNA splicing
Small nucleolar RNA (snoRNA)	70–100	Sequence-specific methylation of rRNA

Table 26-1

Translation: The Genetic Code

Recall: Genetic Code is Degenerate & Nonrandom

Gold = hydrophobic amino acids; pyrimidine at second position

Polar amino acids (blue = basic; red = acidic; purple = uncharged polar) have purine at second position

How was the Triplet code discovered?

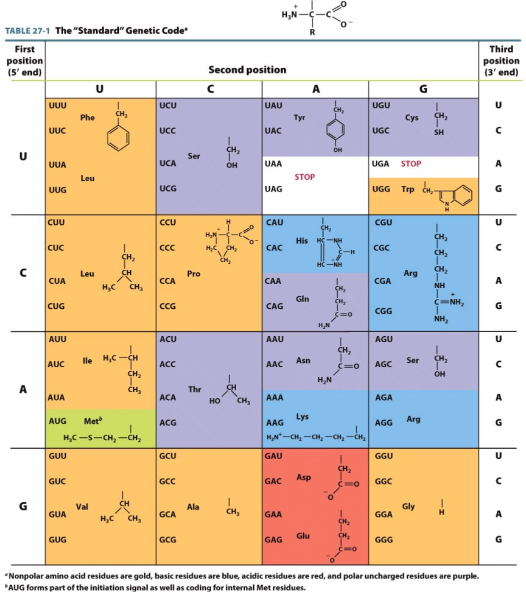


TABLE 27-1 **The "Standard" Genetic Code**[a]

First position (5′ end)	Second position				Third position (3′ end)
	U	C	A	G	
U	UUU Phe	UCU Ser	UAU Tyr	UGU Cys	U
	UUC	UCC	UAC	UGC	C
	UUA Leu	UCA	UAA STOP	UGA STOP	A
	UUG	UCG	UAG	UGG Trp	G
C	CUU Leu	CCU Pro	CAU His	CGU Arg	U
	CUC	CCC	CAC	CGC	C
	CUA	CCA	CAA Gln	CGA	A
	CUG	CCG	CAG	CGG	G
A	AUU Ile	ACU Thr	AAU Asn	AGU Ser	U
	AUC	ACC	AAC	AGC	C
	AUA	ACA	AAA Lys	AGA Arg	A
	AUG Met[b]	ACG	AAG	AGG	G
G	GUU Val	GCU Ala	GAU Asp	GGU Gly	U
	GUC	GCC	GAC	GGC	C
	GUA	GCA	GAA Glu	GGA	A
	GUG	GCG	GAG	GGG	G

[a] Nonpolar amino acid residues are gold, basic residues are blue, acidic residues are red, and polar uncharged residues are purple.

[b] AUG forms part of the initiation signal as well as coding for internal Met residues.

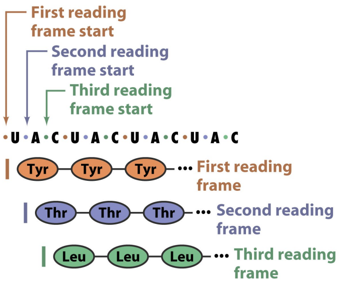
Translation: The Genetic Code

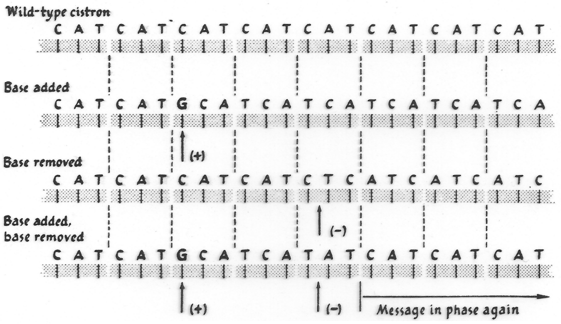
ORFs

THE ~~B~~IG RED FOX ATE THE EGG

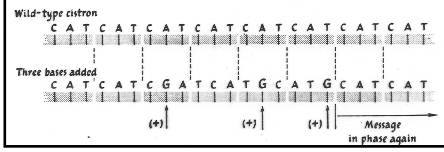
If one base is deleted: THE IGR EDF OXA TET HEE GG

If one base is then inserted: THE IGR EDX FOX ATE THE EGG





Brenner & Crick Experiment:



The regain of function for the triple mutant told Brenner and Crick that it was a triplet code, uninterrupted.

How was the code deciphered?

Translation: The Genetic Code

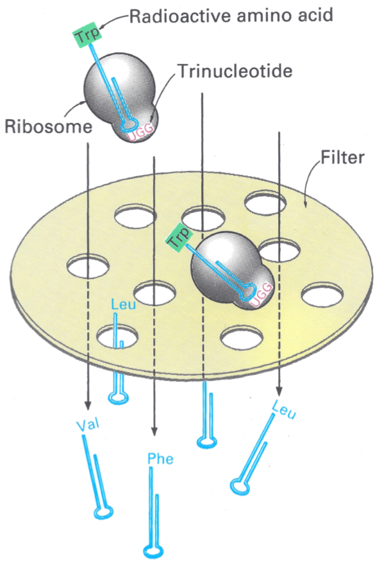
Key Developments:

1. **Chemical synthesis of nucleic acids**
2. **<u>in vitro</u> protein synthesis**

Nirenberg (NIH)

1. First codons used Polynucleotide Phosphorylase (NDP $\rightleftharpoons$ RNA + P_i) to make RNA in vitro: poly-A, poly-C, etc.

Result:
UUU=Phe, AAA=Lys,
CCC=Pro, GGG=Gly



2. Chemical synthesis of defined triplets.
   - Use ribosomes and charged tRNA with different radioactive amino acids
   - Mix and filtrate - only those amino acids with correct tRNA to complementary “mRNA” will complex with the ribosome

Result: 50/64 determined

Translation: The Genetic Code

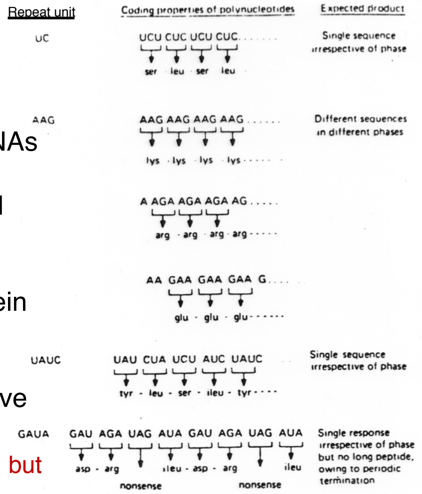
Key Developments:

1. **Chemical synthesis of nucleic acids**
2. **in vitro protein synthesis**

Khorana (MIT)

- Chemical synthesis of repetitive RNAs by first making small overlapping complementary DNAs, ligating, and using RNA polymerase to make corresponding repetitive RNAs.
- Add synthetic RNAs to in vitro protein synthesis cocktail with radioactive amino acids.
- Analyze sequences of the radioactive protein produced.

Result: nearly all codons determined, but some remained ambiguous.
Combined data from Nirenberg established the CODE.
This method was only one able to determine the stop codons.



Use of repeat polynucleotides for determining the genetic code. The polynucleotides were used as messengers in vitro in conjunction with a protein-synthesizing system from *E. coli*. The polypeptide chains produced were isolated and analyzed, and their composition defined the coding properties of the contributing triplets. (Adapted from Khorana G: Harvey Lect 62:79, 1968)

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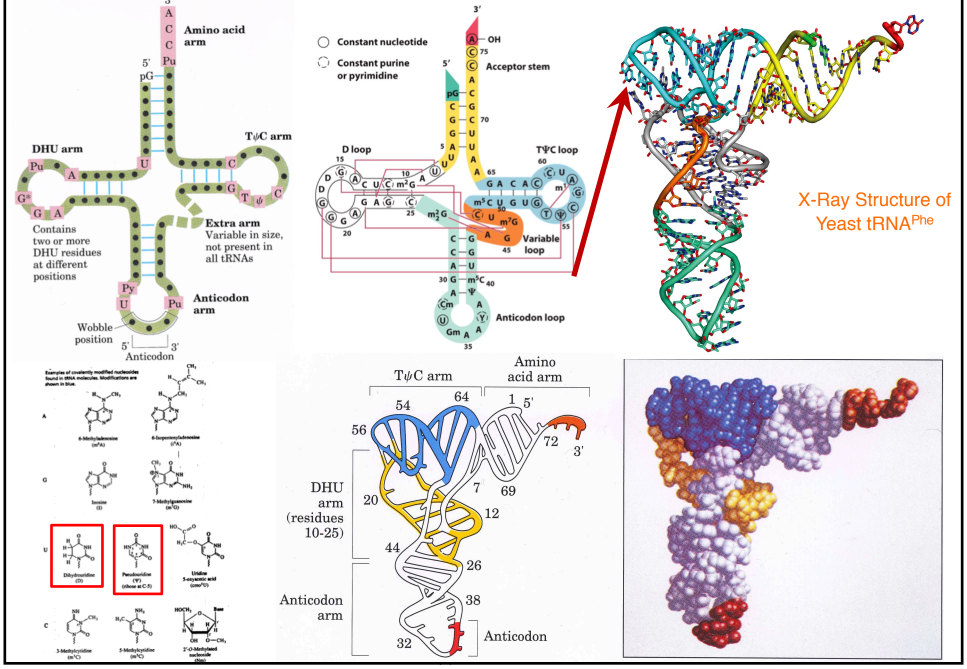
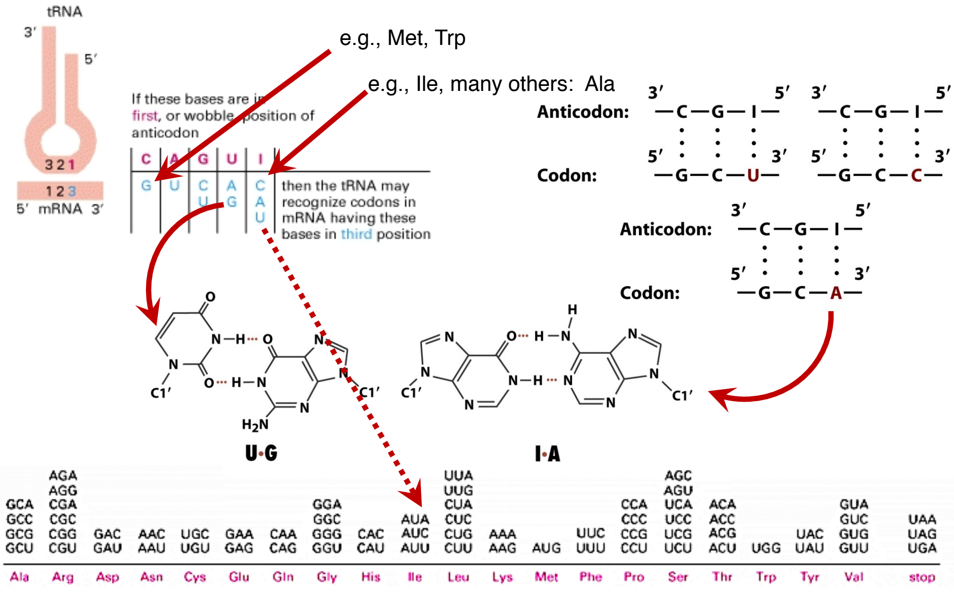
Translation: tRNA



Translation: tRNA

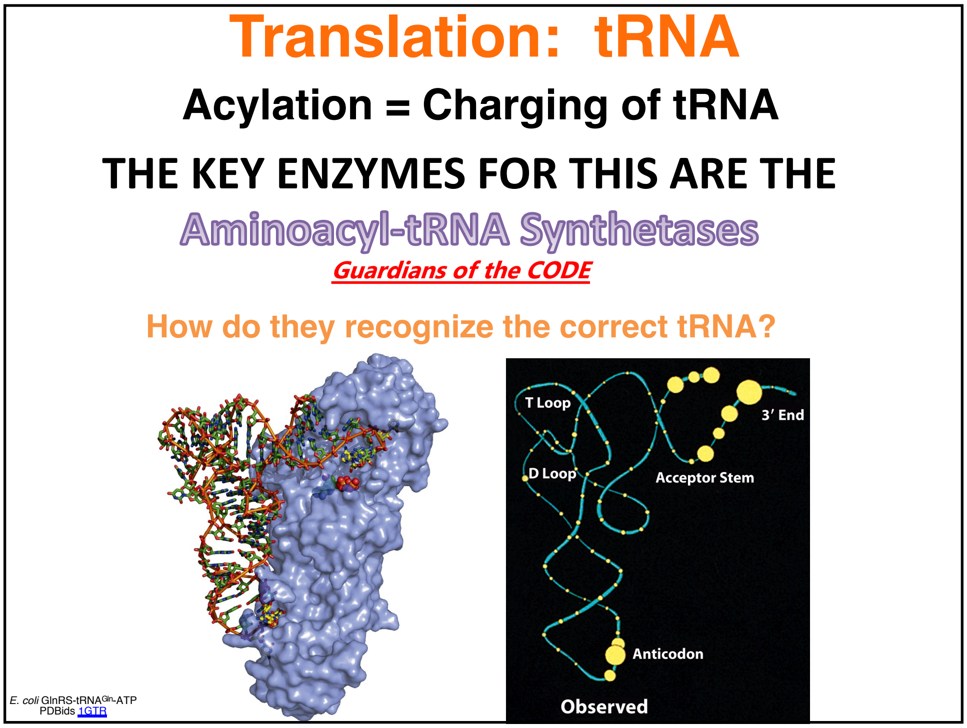
tRNA anticodon-codon interactions



e.g., Met, Trp

e.g., Ile, many others: Ala

GCA GCC GCG GCU	AGA AGG CGA CGC CGG CGU	GAC GAU	AAC AAU	UGC UGU	GAA GAG	CAA CAG	GGA GGC GGG GGU	CAC CAU	AUA AUC AUU	UUA UUG CUA CUC CUG CUU	AAA AAG	AUG	UUC UUU	CCA CCC CCG CCU	AGC AGU UCA UCC UCG UCU	ACA ACC ACG ACU	UGG	UAC UAU	GUA GUC GUG GUU	UAA UAG UGA
Ala	Arg	Asp	Asn	Cys	Glu	Gln	Gly	His	Ile	Leu	Lys	Met	Phe	Pro	Ser	Thr	Trp	Tyr	Val	stop



Translation: tRNA

Acylation = Charging of tRNA

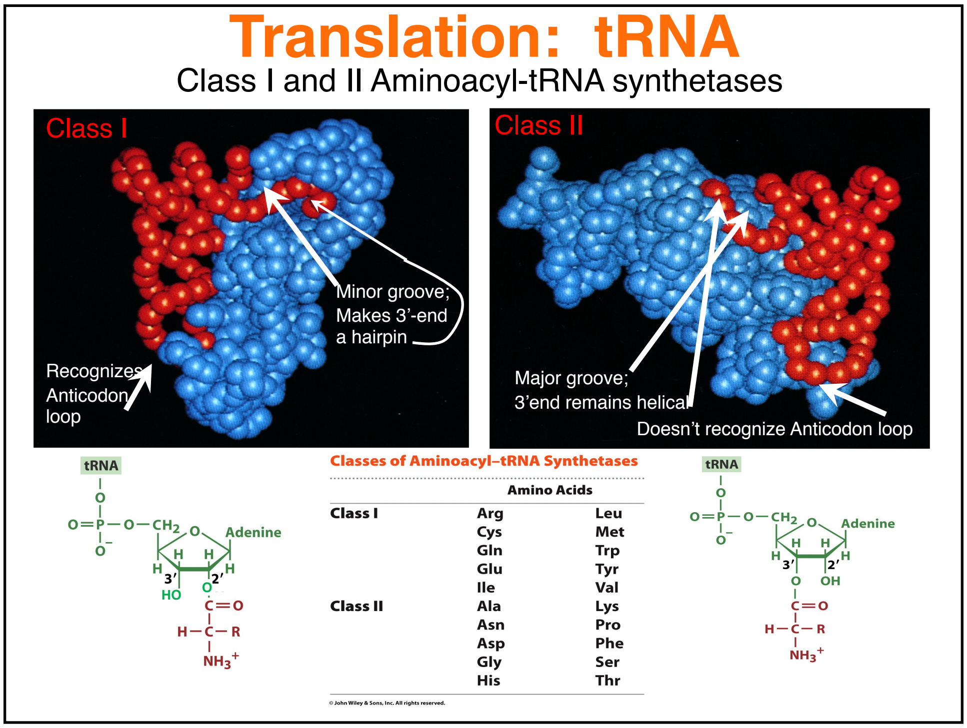
THE KEY ENZYMES FOR THIS ARE THE

Aminoacyl-tRNA Synthetases

Guardians of the CODE

How do they recognize the correct tRNA?

E. coli GlnRS-tRNA^{Gln}-ATP
PDBids 1GTR



Translation: tRNA

Class I and II Aminoacyl-tRNA synthetases

Minor groove; Makes 3'-end a hairpin

Recognizes Anticodon loop

Major groove; 3'end remains helical

Doesn't recognize Anticodon loop

Classes of Aminoacyl–tRNA Synthetases

	Amino Acids	
Class I	Arg	Leu
	Cys	Met
	Gln	Trp
	Glu	Tyr
	Ile	Val
Class II	Ala	Lys
	Asn	Pro
	Asp	Phe
	Gly	Ser
	His	Thr

Translation: tRNA

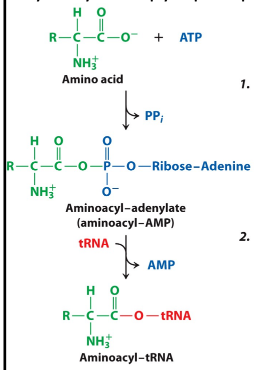
Aminoacylation: 2 steps

2 step reaction:

1) A.A. + ATP → AA-AMP + PP_i
2) AA-AMP + tRNA → AA-tRNA + AMP

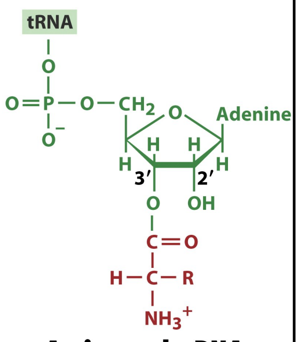
(AA-tRNA is shown at right = “charged” tRNA)

Again, just like with DNA and RNA synthesis, subsequent hydrolysis of pyrophosphate provides driving force for reaction



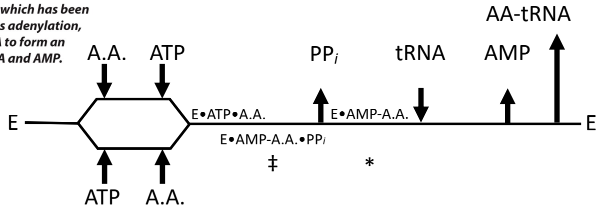
1. The amino acid reacts with ATP to form an aminoacyl–adenylate (aminoacyl–AMP). The subsequent hydrolysis of the PP_i product makes this step irreversible in vivo.

2. The amino acid, which has been “activated” by its adenylation, reacts with tRNA to form an aminoacyl–tRNA and AMP.



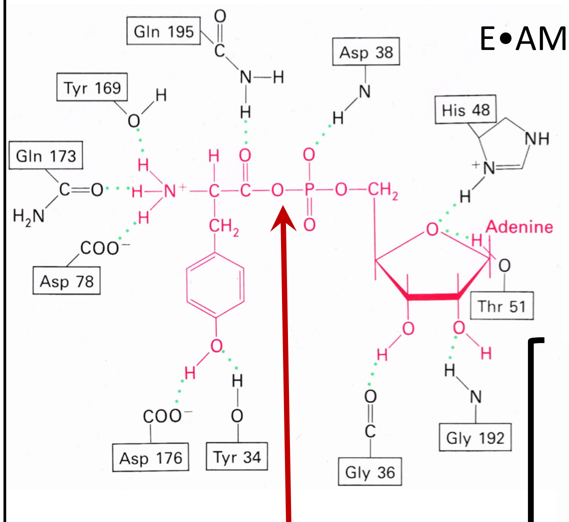
Aminoacyl–tRNA

First ½ reaction is sequential random bi uni



Translation: tRNA

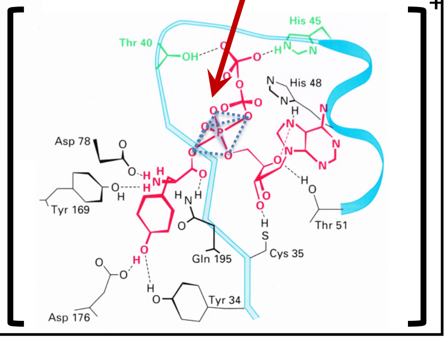
E•AMP-Tyr



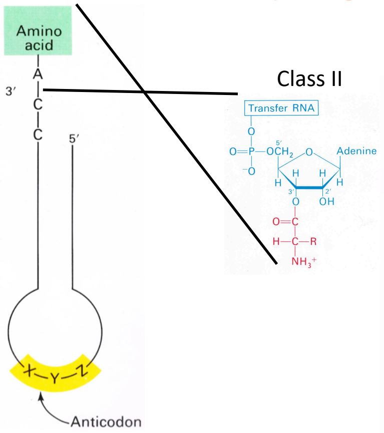
Condensation of two acids = anhydride (mixed)

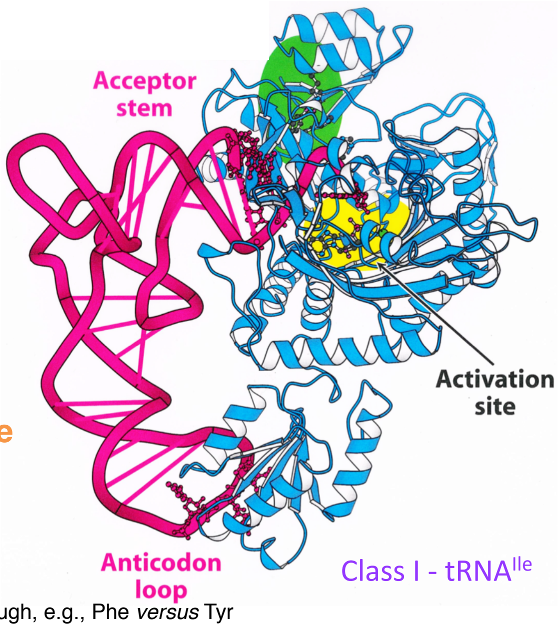
This bi-pyrimidal shape has 180° angle between axial oxygens, which were 109.5° in ATP.

$[E\bullet AMP\sim Tyr\sim PP_i]^\ddagger$



Translation: tRNA



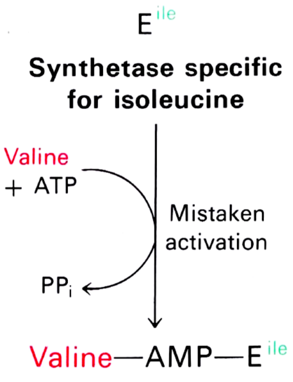


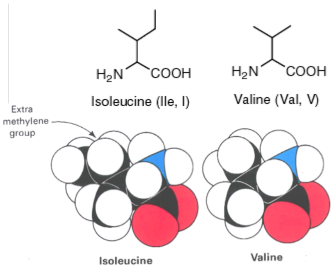
Class I - tRNA^{Ile}

How do they ensure the correct amino acid is attached to the correct tRNA?

Some amino acids are different enough, e.g., Phe *versus* Tyr
(H-bonds from D176 & Y34 to phenolic oxygen account for 150,000 fold stronger binding)

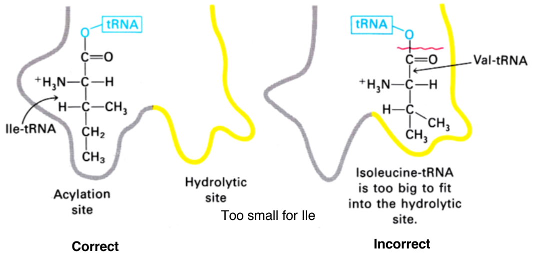
Translation: tRNA



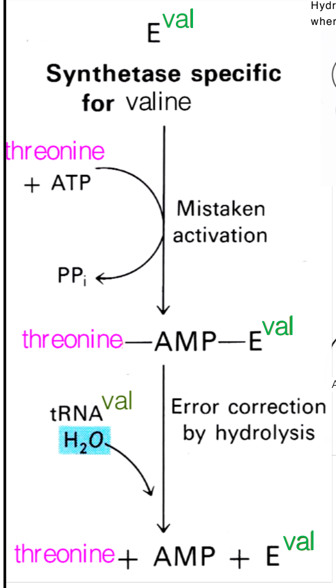


The extra methylene only gets E^{ile} 200-fold stronger binding to Ile *versus* Val.
And [Val] is 5x higher than [Ile].
This cuts the effective driving force to only 40-fold = 2.5% error rate.

The editing site comes to the rescue!
When tRNA^{ile} binds, the Val-AMP is forced into the hydrolysis site.
Ile-AMP is too large to fit.
Decreases the error rate to 0.0003.



Translation: tRNA



E^{val}

Synthetase specific for valine

threonine + ATP

PP_i

Mistaken activation

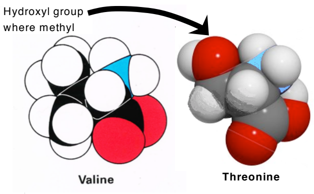
threonine—AMP—E^{val}

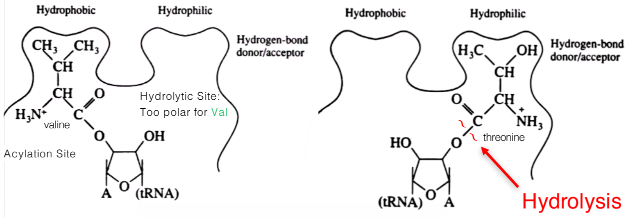
$tRNA^{val}$

H_2O

Error correction by hydrolysis

threonine + AMP + E^{val}





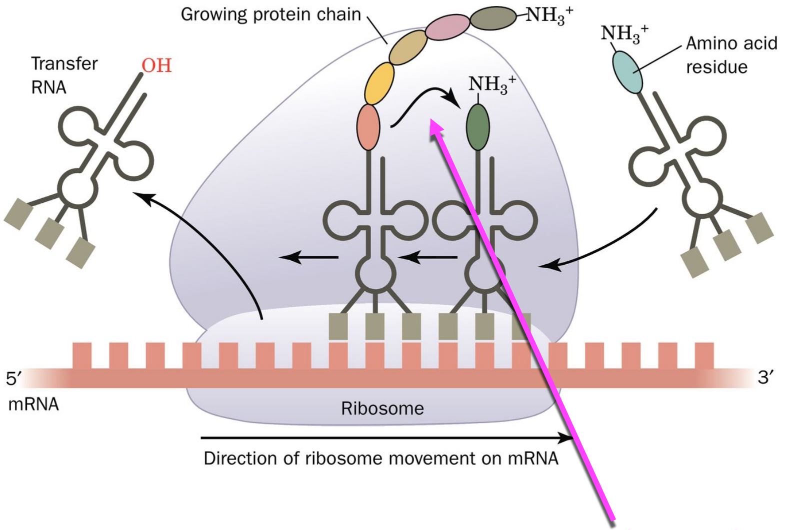
Proposed mechanism for the prevention of the misacylation of $tRNA^{Val}$ with threonine. The valyl tRNA synthetase is thought to have two distinct sites: an acylation site where the amino acid is transferred from the adenylate to the tRNA and a hydrolysis site where amino acids that bind tightly are hydrolyzed from the tRNA. *A:* The acylation site is imagined to be specific for valine by being hydrophobic and complementary in shape to the valine side chain. *B:* The hydrolytic site is depicted as being specific for threonine by virtue of a hydrogen-bond donor or acceptor for its hydroxyl group; binding to this site produces hydrolysis of the charged tRNA. (From A. R. Fersht and M. Kaethner, *Biochemistry* 15:3342–3346, 1976.)

Transcription & Translation

Transcription
- Overview
- Process
- RNA Polymerase
- Fidelity

Translation
- Genetic Code
  - triplet
  - decyphering
- tRNA
  - Structure
  - Anticodon
  - Acylation (charging)
    - Aminoacyl-tRNA Synthetases
    - Mechanism
    - Fidelity
- Protein Biosynthesis
  - Overview
  - Process
  - Ribosome review
  - Elongation
    - Decoding: Fidelity
    - Peptidyl Transferase
  - Energy

Translation: Protein Biosynthesis



Making the Peptide Bond

Translation: Protein Biosynthesis

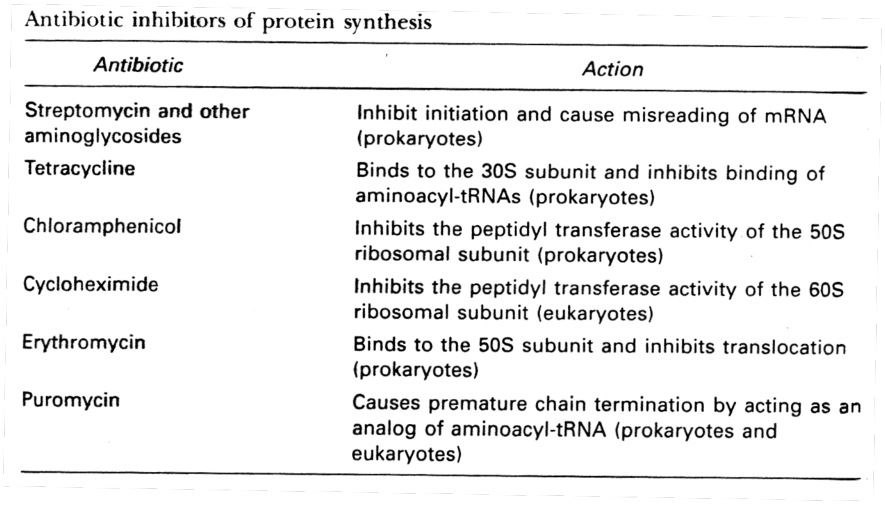
Process:

- **Initiation**
- **Elongation**
  1. **Decoding**
  2. **Peptidyl Transferase**
  3. **Translocation**
- **Termination**

Fidelity

Making the Peptide Bond

Translation: Protein Biosynthesis

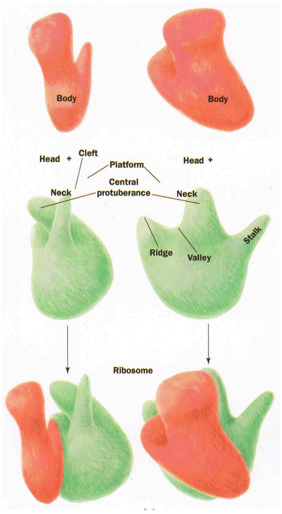


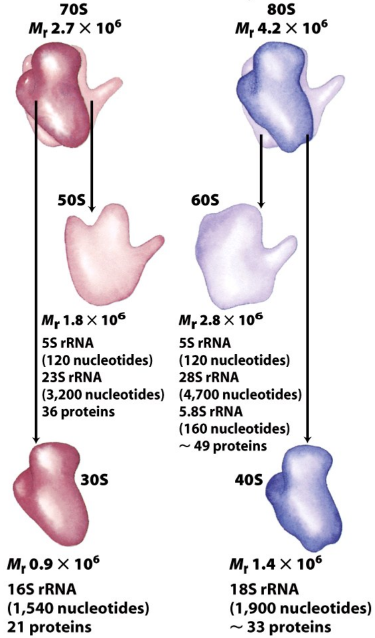
Antibiotic inhibitors of protein synthesis

Antibiotic	*Action*
Streptomycin and other aminoglycosides	Inhibit initiation and cause misreading of mRNA (prokaryotes)
Tetracycline	Binds to the 30S subunit and inhibits binding of aminoacyl-tRNAs (prokaryotes)
Chloramphenicol	Inhibits the peptidyl transferase activity of the 50S ribosomal subunit (prokaryotes)
Cycloheximide	Inhibits the peptidyl transferase activity of the 60S ribosomal subunit (eukaryotes)
Erythromycin	Binds to the 50S subunit and inhibits translocation (prokaryotes)
Puromycin	Causes premature chain termination by acting as an analog of aminoacyl-tRNA (prokaryotes and eukaryotes)

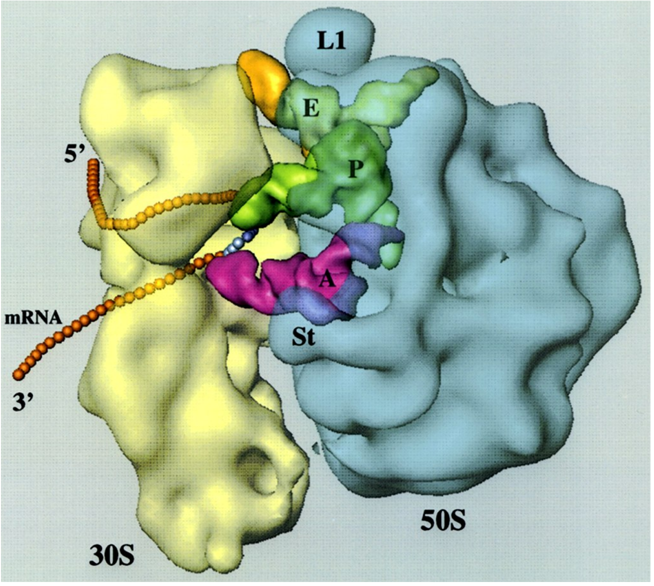
Translation: Protein Biosynthesis

Ribosome: RNA-protein complex





Translation: Protein Biosynthesis



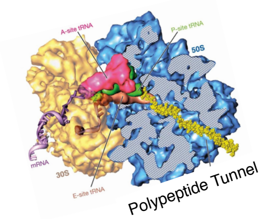
Process Overview:
- mRNA read in 5'→3' direction
- protein synthesized from N-terminus to C-terminus
- protein chain elongation occurs by transferring new AA to C-terminus of growing chain

Ribosome has 3 tRNA binding sites:

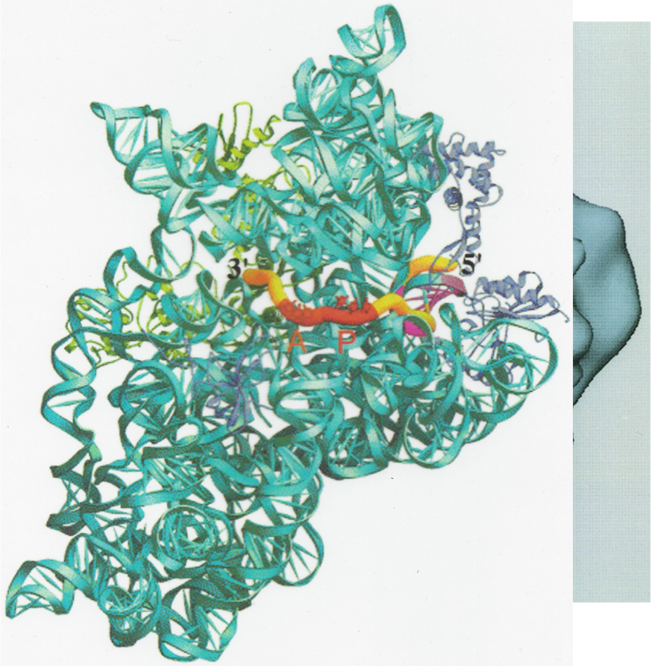
A-site – **a**mino acyl tRNA binding site

P-site – **p**eptidyl-tRNA binding site

E-site – **e**xit site, deacylated tRNA



Translation: Protein Biosynthesis



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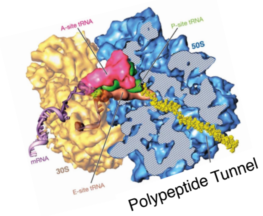
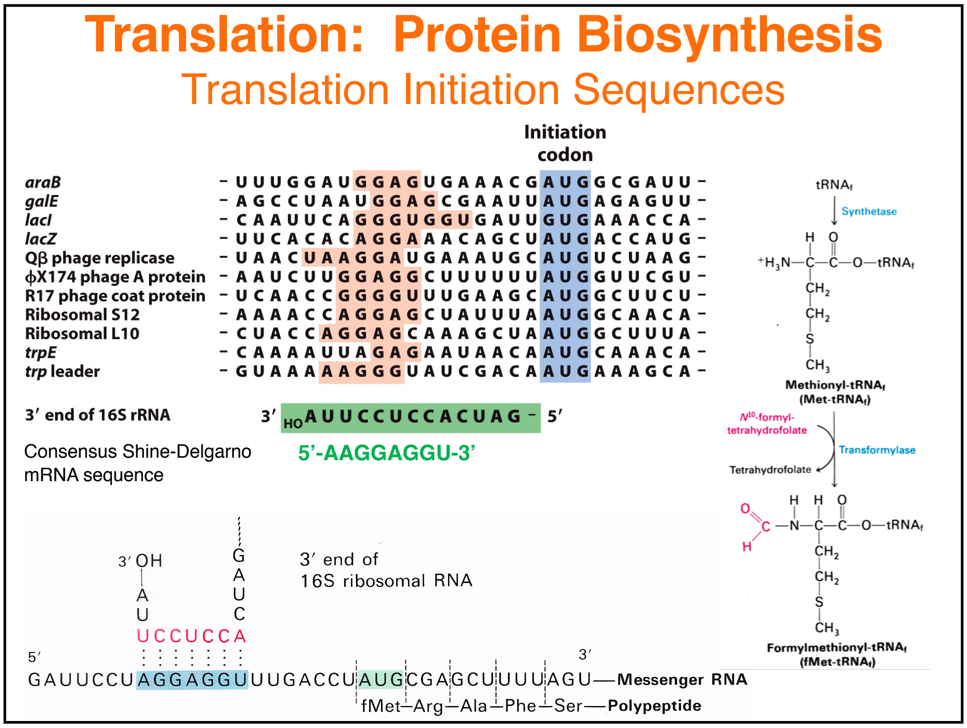




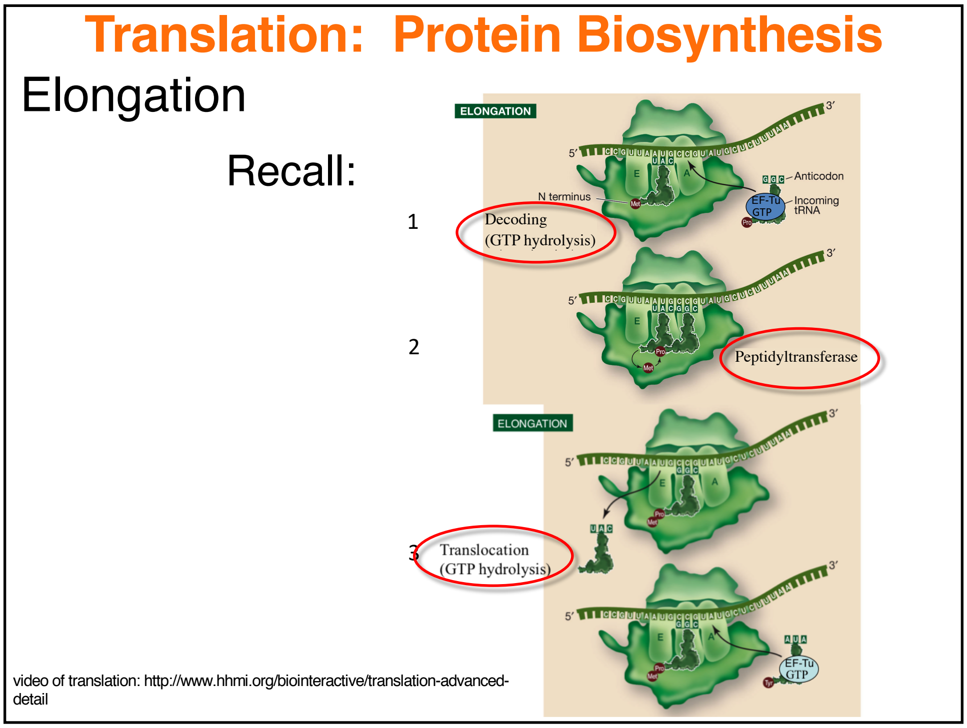
Translation: Protein Biosynthesis

Translation Initiation Sequences

	Initiation codon
araB	– U U U G G A U G G A G U G A A A C G A U G G C G A U U –
galE	– A G C C U A A U G G A G C G A A U U A U G A G A G U U –
lacI	– C A A U U C A G G G U G G U G A U U G U G A A A C C A –
lacZ	– U U C A C A C A G G A A A C A G C U A U G A C C A U G –
Qβ phage replicase	– U A A C U A A G G A U G A A A U G C A U G U C U A A G –
ϕX174 phage A protein	– A A U C U U G G A G G C U U U U U A U G G U U C G U –
R17 phage coat protein	– U C A A C C G G G G U U U G A A G C A U G G C U U C U –
Ribosomal S12	– A A A A C C A G G A G C U A U U U A A U G G C A A C A –
Ribosomal L10	– C U A C C A G G A G C A A A G C U A A U G G C U U U A –
trpE	– C A A A A U U A G A G A A U A A C A A U G C A A A C A –
trp leader	– G U A A A A A G G G U A U C G A C A A U G A A A G C A –

3′ end of 16S rRNA 3′ $_{HO}$**AUUCCUCCACUAG** – 5′

Consensus Shine-Delgarno mRNA sequence **5’-AAGGAGGU-3’**



Translation: Protein Biosynthesis

Elongation

Recall:

1 Decoding (GTP hydrolysis)

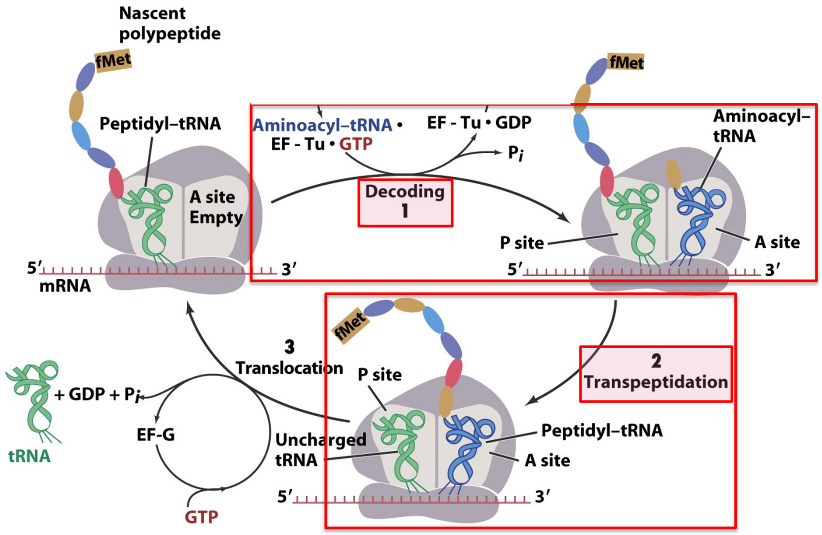
2 Peptidyltransferase

3 Translocation (GTP hydrolysis)

video of translation: http://www.hhmi.org/biointeractive/translation-advanced-detail

Translation: Protein Biosynthesis

Elongation



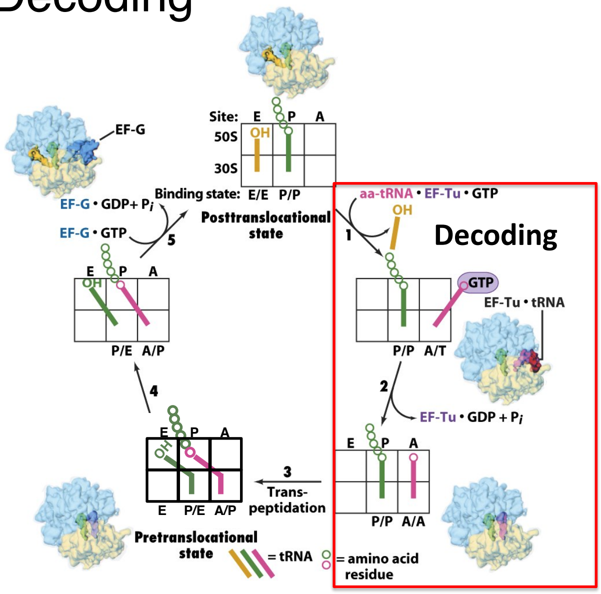
Translation: Protein Biosynthesis

Elongation: Decoding

EF-Tu:

- Most abundant protein
- Binds to AA-tRNA (not free tRNA)
- Anti-codon end is free to bind to 30S-mRNA.

Kinetic proofreading: GTP hydrolysis



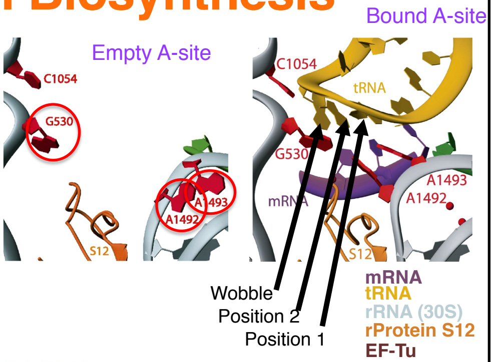
Translation: Protein Biosynthesis

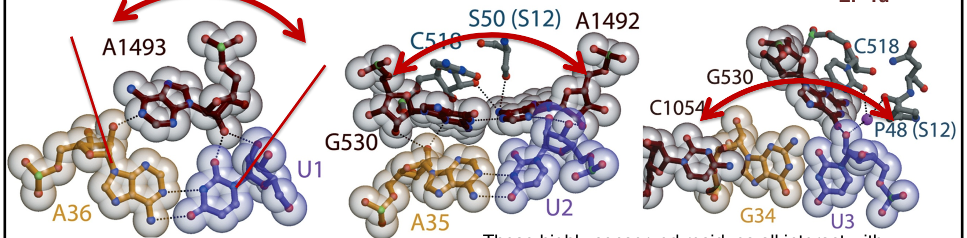
Elongation: Decoding

5'-UUU
3'-AAG

Three highly conserved residues on the 30S subunit each associate with the tRNA anticodon residues:

- Position 1 (U1): A^{1493}
- Position 2 (U2): A^{1492}
- Position 3 (Wobble) (U3): G^{530}





These highly conserved residues all interact with the minor groove!!
Where have we seen this before?

Minor groove

The energetics of these binding interactions is insufficient to account for the error rate of protein synthesis….

Translation: Protein Biosynthesis

Elongation: Fidelity

How does the EF-Tu•GTP•AA-tRNA•mRNA•Ribosome Complex examine this codon-anticodon interaction via a second method?

(much like DNA polymerases and aminoacyl-tRNA synthetases)

It uses a complex of EF-Tu•GDP•AA-tRNA•mRNA•Ribosome to test the codon-anticodon interaction via a conformational change that stresses this interaction.

- EF-Tu•GTP•AA-tRNA binds the A-site with a strained anticodon stem-loop
- Anticodon-codon interactions in the A-site induce EF-Tu's hydrolysis of GTP to GDP. GTP hydrolysis is FASTER for cognate tRNA.
- This results in EF-Tu release from the complex as EF-Tu•GDP

- Once the EF-Tu is gone, the AA-tRNA relaxes, swings its acceptor stem into the A-site on the 50S, pivoting at the codon-anticodon interaction
- Non-cognate tRNAs do not survive this pivot and fall out most of the time

THEREFORE, GTP HYDROLYSIS IS KEY:

1. In its slowness, time is allowed for optimal cognate codon-anticodon interactions
2. In its hydrolysis, initiated by these interactions, the process achieves a second test of the fitness by being "hinged" at the codon-anticodon during the pivoting.

Translation: Protein Biosynthesis

Frequency of inserting an incorrect amino acid	*Probability of synthesizing an error-free protein*		
	Number of amino acid residues		
	100	*300*	*1000*
10^{-2}	0.366	0.049	0.000
10^{-3}	0.905	0.741	0.368
10^{-4}	0.990	0.970	0.905
10^{-5}	0.999	0.997	0.990

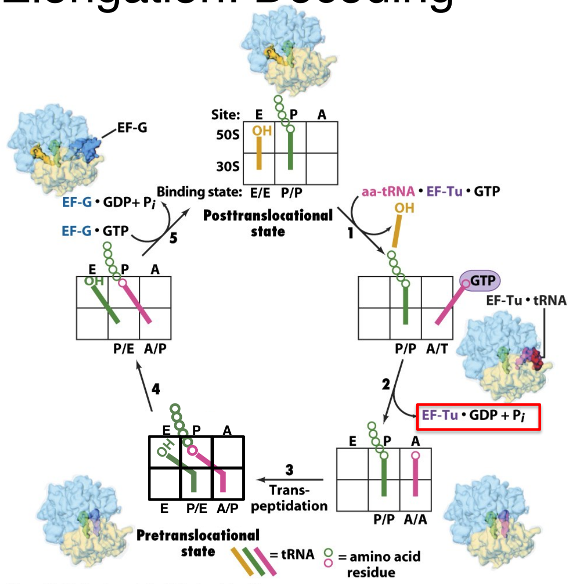
$$p = (1 - \varepsilon)^n$$

p is the probability of an error-free protein
ε is the error rate
n is the length of the protein

Each of the 2 selection mechanisms (EF-Tu GTPase and conf. change) have a 1% error rate ($\varepsilon = 10^{-2}$). Combined $\varepsilon = 10^{-4}$.

Translation: Protein Biosynthesis

Elongation: Decoding

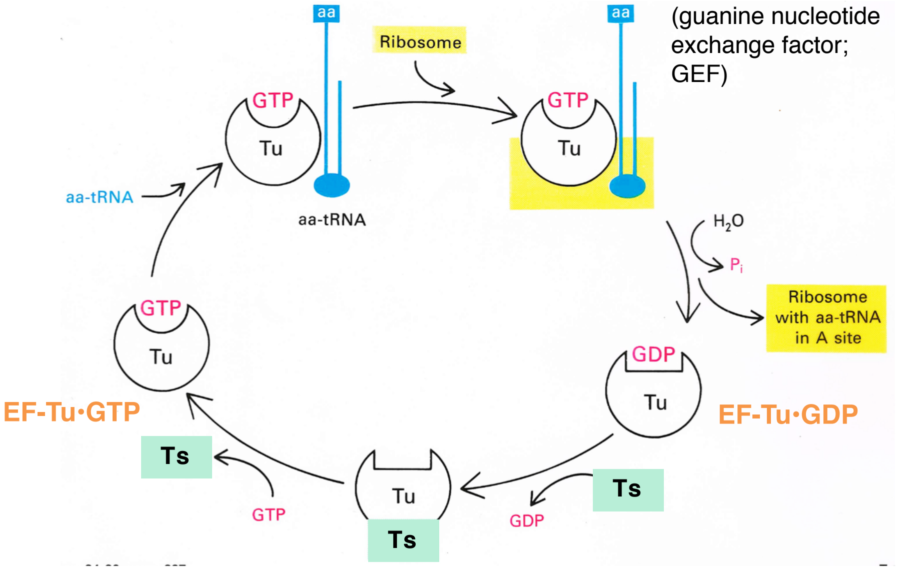


What happens to EF-Tu·GDP?

Translation: Protein Biosynthesis

Elongation: Decoding

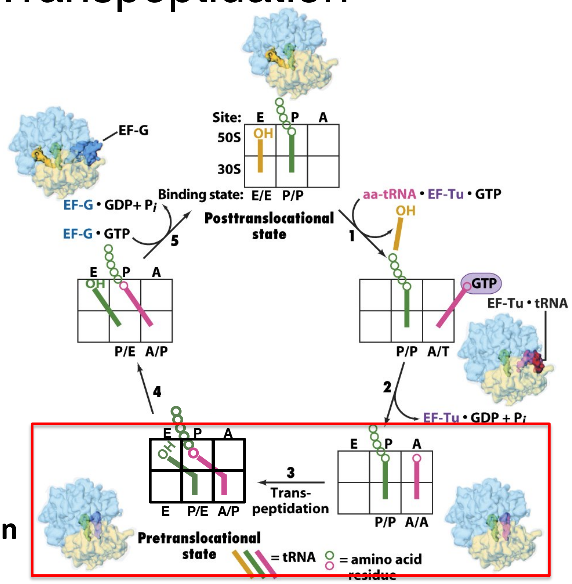
EF-Ts is a GTP exchange protein (guanine nucleotide exchange factor; GEF)



Translation: Protein Biosynthesis

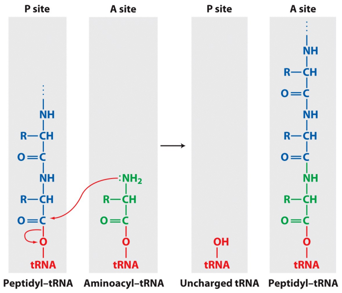
Elongation: Transpeptidation

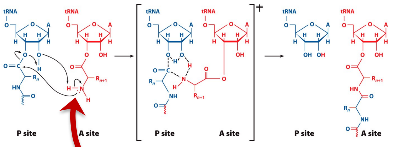
Transpeptidation



Translation: Protein Biosynthesis

Elongation: Transpeptidation or the Peptidyltransferase reaction

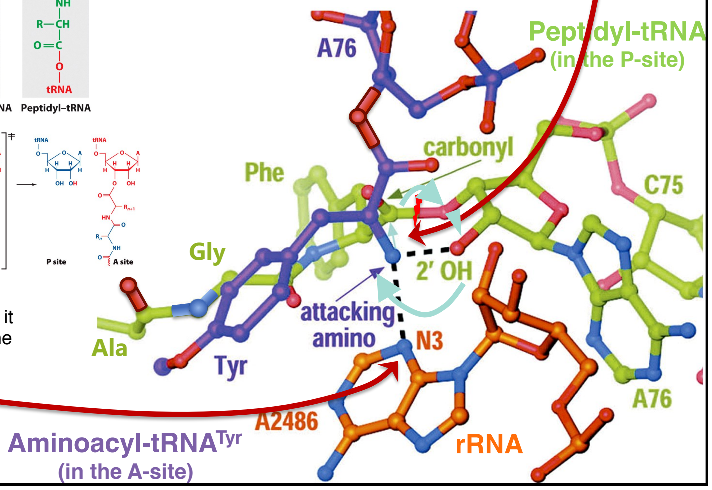




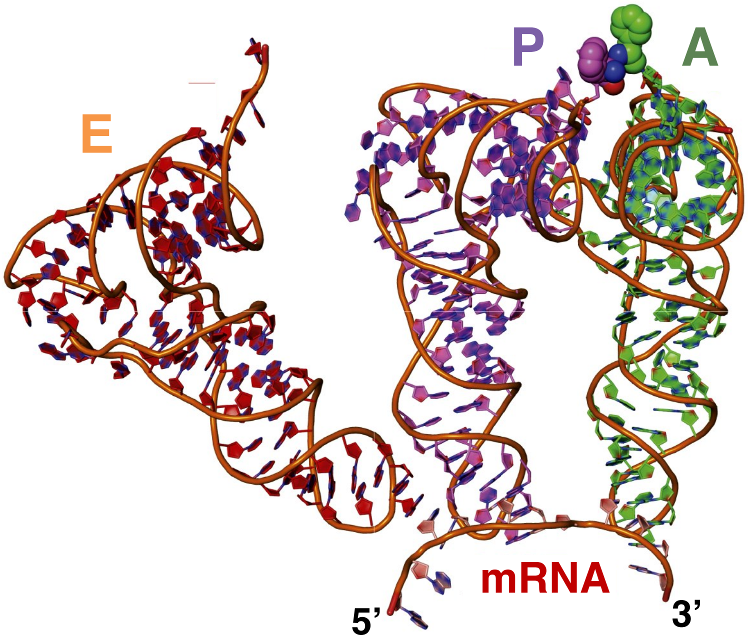
Polarization of α-amino of incoming amino acid to make it a better nucleophile is from the N3 of Adenine^{2486} of the large rRNA.

It's a RIBOZYME!!

Rate enhancement is mostly all proximity (entropy trap)



mRNA Interactions with tRNAs



Interactions of tRNA with mRNA
PDBid 2WDK

Translation: Protein Biosynthesis

ENERGY REQUIREMENTS:

• 2 ATP equivalents for every base in the 3-base codon of the mRNA (mRNA synthesis (transcription))	= 6
• 2 ATP equivalents for every AA-tRNA (tRNA charging)	= 2
• 1 ATP equivalent for binding with EF-Tu	= 1
• 1 ATP equivalent for translocation with EF-G	= 1
	= 10 total ATPs for every residue