Hidden Markov Models

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Many pages are from Ben Langmead

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Problem two: given a genome, search for CpG islands in the genome.

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ATCATGCTGGAAATTGAAGAGGAACGCAGCCAGTGGCTTGGCAGAGATCACTGAGGATAATCAGACCTCAGGTTGCAGAAGACAGTGGGACAACATCACGT
GCTGGCCTGAGGCGCAGGTGGGAGCAGTTGTGGTGAAGCCATGCCCAAAGTACTTCAGGTTCCTCACCACTTTTCTCGGAAATGTGAGCAGGAATTGCAC
AAGTCAGGGCTGGACAGATGTGTACCCTGCACCGTATGCTGTTGCTTGTGGATACGATTCCAACAGCACACCAGGGGAAGAGCAAACGGCGTTCTATGGC
ACGGTCAAGACCGGCTACACCATTGGACATACCTTGTCACTCATTGCTCTCACAGCTGCTATGATCATTTTCTGTCTCTTCAGAAAACTACACTGTACTC
GAAATTATATTCATATGCACCTCTTCATGTCCTTTATAATGAGAGCCATTGCAGTCTTCCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGC
GCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGC
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CTGAGGCCCGTGATGGCTGGCACTACGGAGAGAGTGAGAAGACCAAGATGCGGGGCTGGTTTCCCTTCTCCTACACCCGGGTCCTGGACAGCGACGGCAG
TGACAGGCTGCACATGAGCTTGCAGCAAGGGAAGAGCAGCAGCACGGGCAACCTCCTAGACAAGGACGACTTGGCCATCCCGCCCCCTGACTACGGCGCC
ACCTCCCGGGCCTTCCCTGCCCAGACAGCCAGTGGCTTCAAGCAGAGGCCCTACAGCGTGGCCGTGCCTGCCTTCTCCCAGGGTCTGGAAGACTATGGAG
CACGGTCCATGAGCAGTGGCAGCGGCACG

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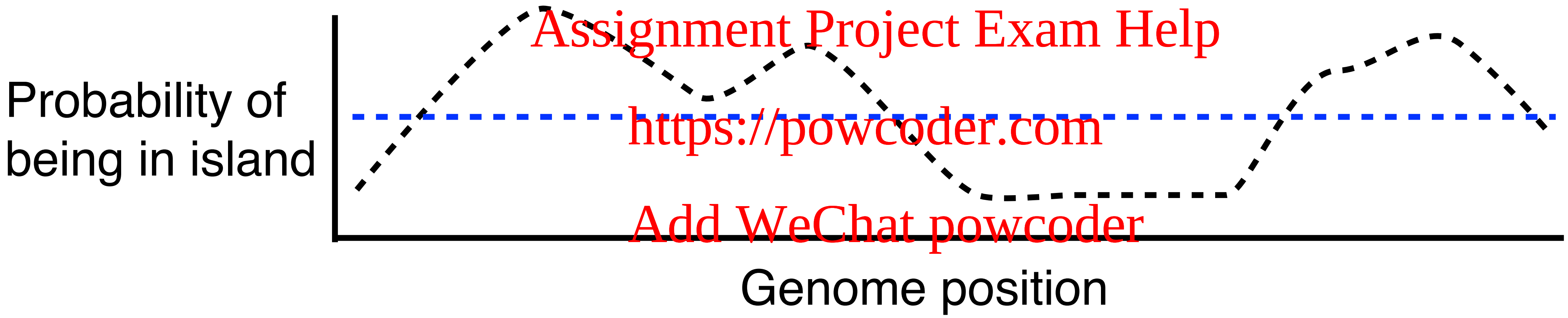
Sequence models

Can we use Markov chains to pick out CpG islands from the rest of the genome?

Markov chain assigns a score to a string; doesn't naturally give a "running" score across a long sequence



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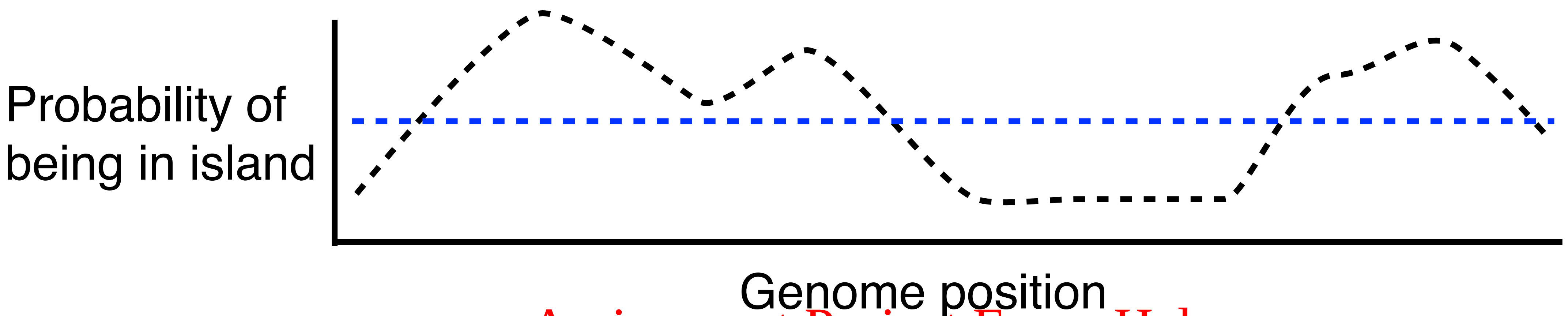
We could use a *sliding window*

(a) Pick window size *w*, (b) score every *w*-mer using Markov chains, (c) use a cutoff to find islands

Smoothing before (c) might also be a good idea

Sequence models



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Choosing *w* involves an assumption about how long the islands are

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- If *w* is too large, we'll miss small islands

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- If *w* is too small, we'll get many small islands where perhaps we should see fewer larger ones

In a sense, we want to switch *between Markov chains* when entering or exiting a CpG island

Ideal solution: every base (rather than a window) is assigned with a label, inside or outside

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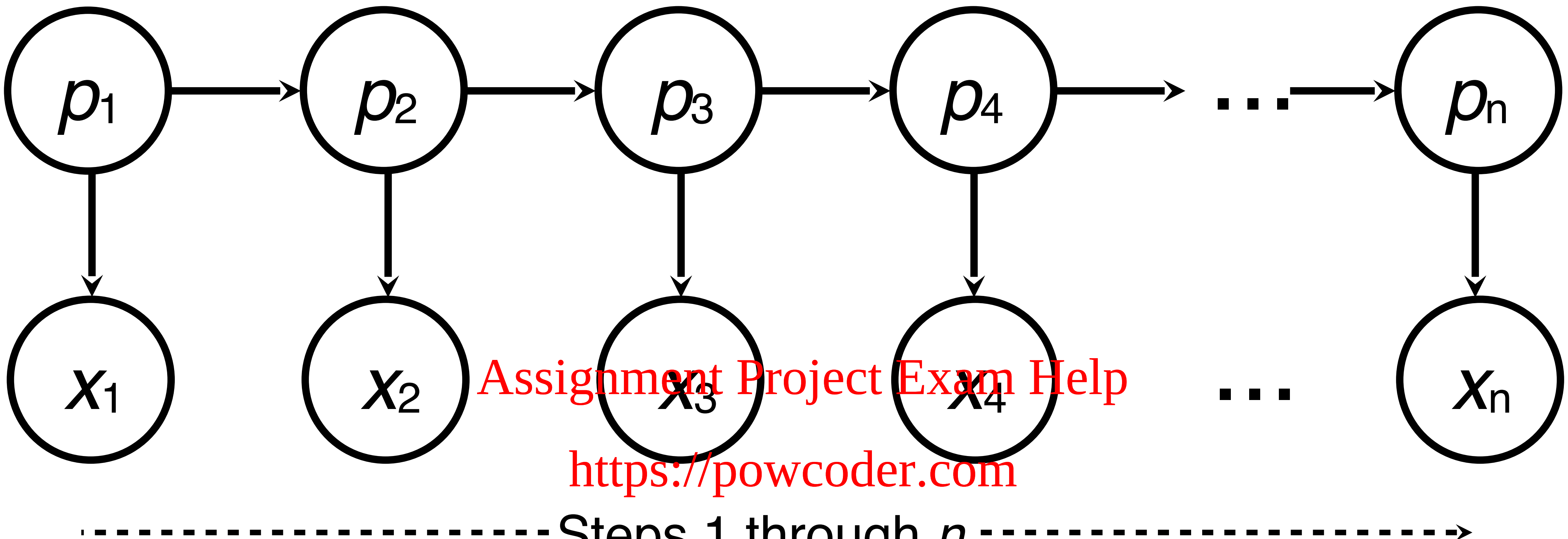
Hidden Markov Model

Trellis diagram



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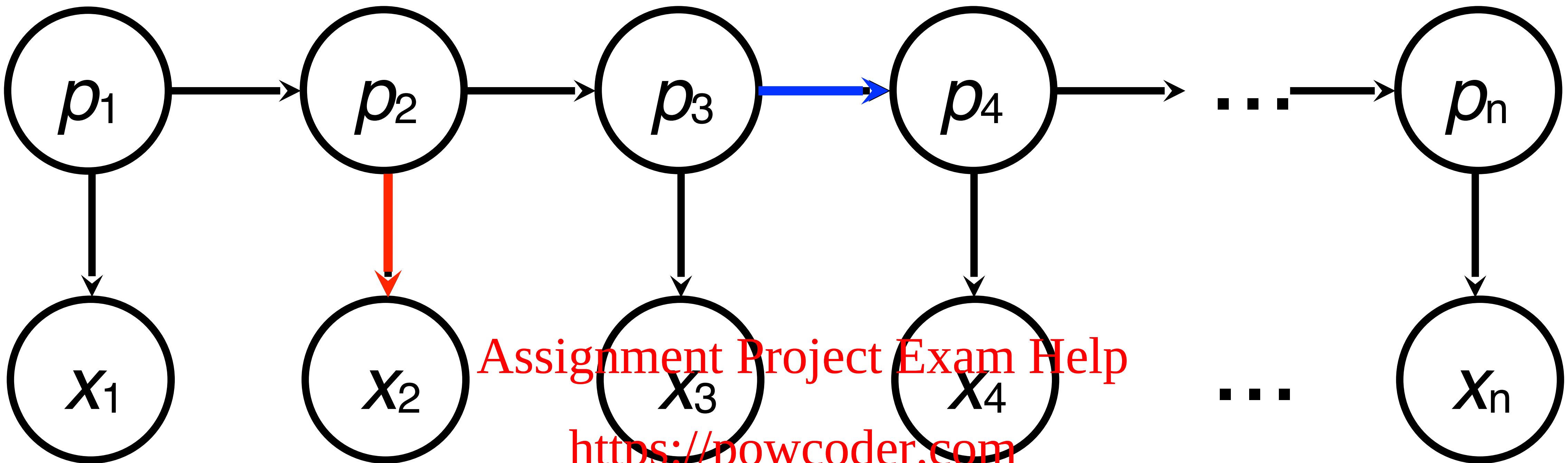
$p = \{ p_1, p_2, ..., p_n \}$ is a sequence of *states* (AKA a *path*). Each p_i takes a value from set Q. We ***do not*** observe p.

$x = \{ x_1, x_2, ..., x_n \}$ is a sequence of *emissions.* Each x_i takes a value from set Σ. We ***do*** observe x.

Our goal: given the observation $x_1, x_2, \ldots x_n$, derive the hidden states $p_1, p_2, p_3, \ldots, p_n$

Hidden Markov Model



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Like for Markov chains, edges capture conditional independence:

x_2 is conditionally independent of everything else given p_2

p_4 is conditionally independent of everything else given p_3

Probability of being in a particular state at step *i* is known once we know what state we were in at step *i*-1. Probability of seeing a particular emission at step *i* is known once we know what state we were in at step *i*.

Hidden Markov Model

Example: occasionally dishonest casino

Dealer repeatedly flips a coin. Sometimes the coin is *fair*, with P(heads) = 0.5, sometimes it's *loaded*, with P(heads) = 0.8. Dealer occasionally switches coins, invisibly to you.

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How does this map to an HMM?

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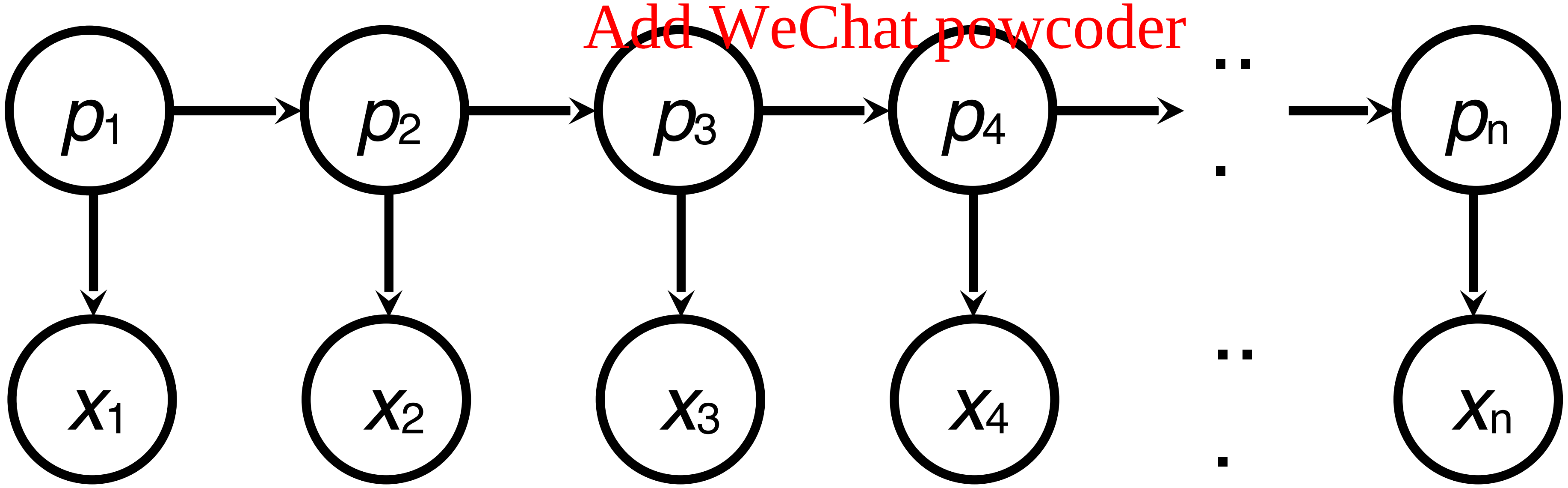

Hidden Markov Model

Example: occasionally dishonest casino

Dealer repeatedly flips a coin. Sometimes the coin is *fair*, with P(heads) = 0.5, sometimes it's *loaded*, with P(heads) = 0.8. Dealer occasionally switches coins, invisibly to you.

How does this map to an HMM?

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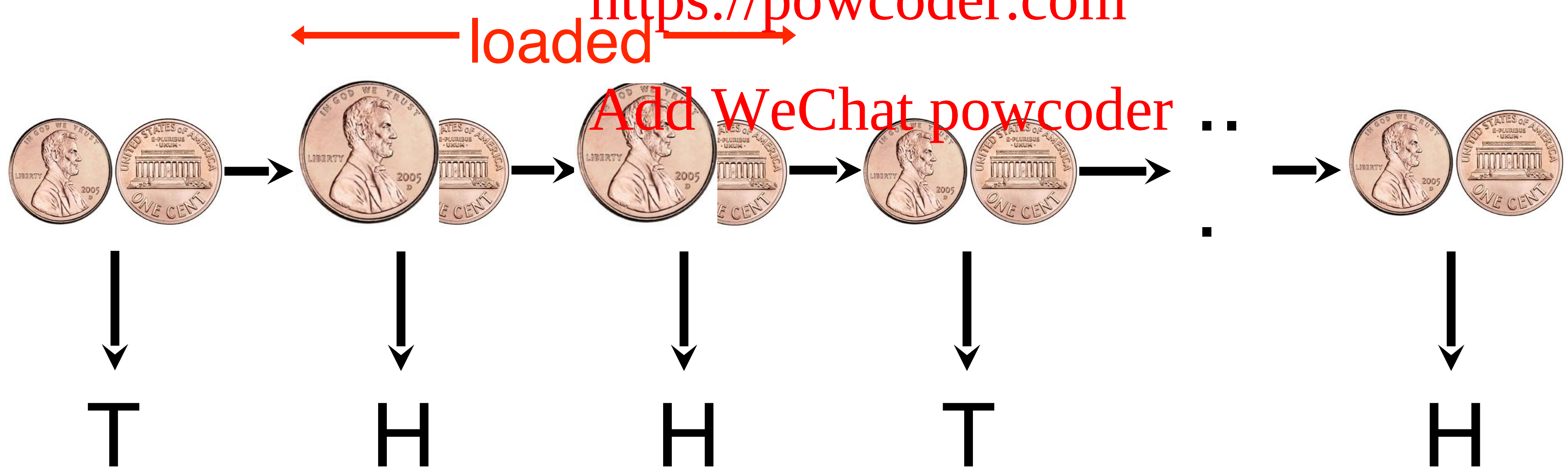


Emissions encode flip outcomes (observed), states encode loadedness (hidden)

We can use HMM to estimate what coin the dealer is using for each flip

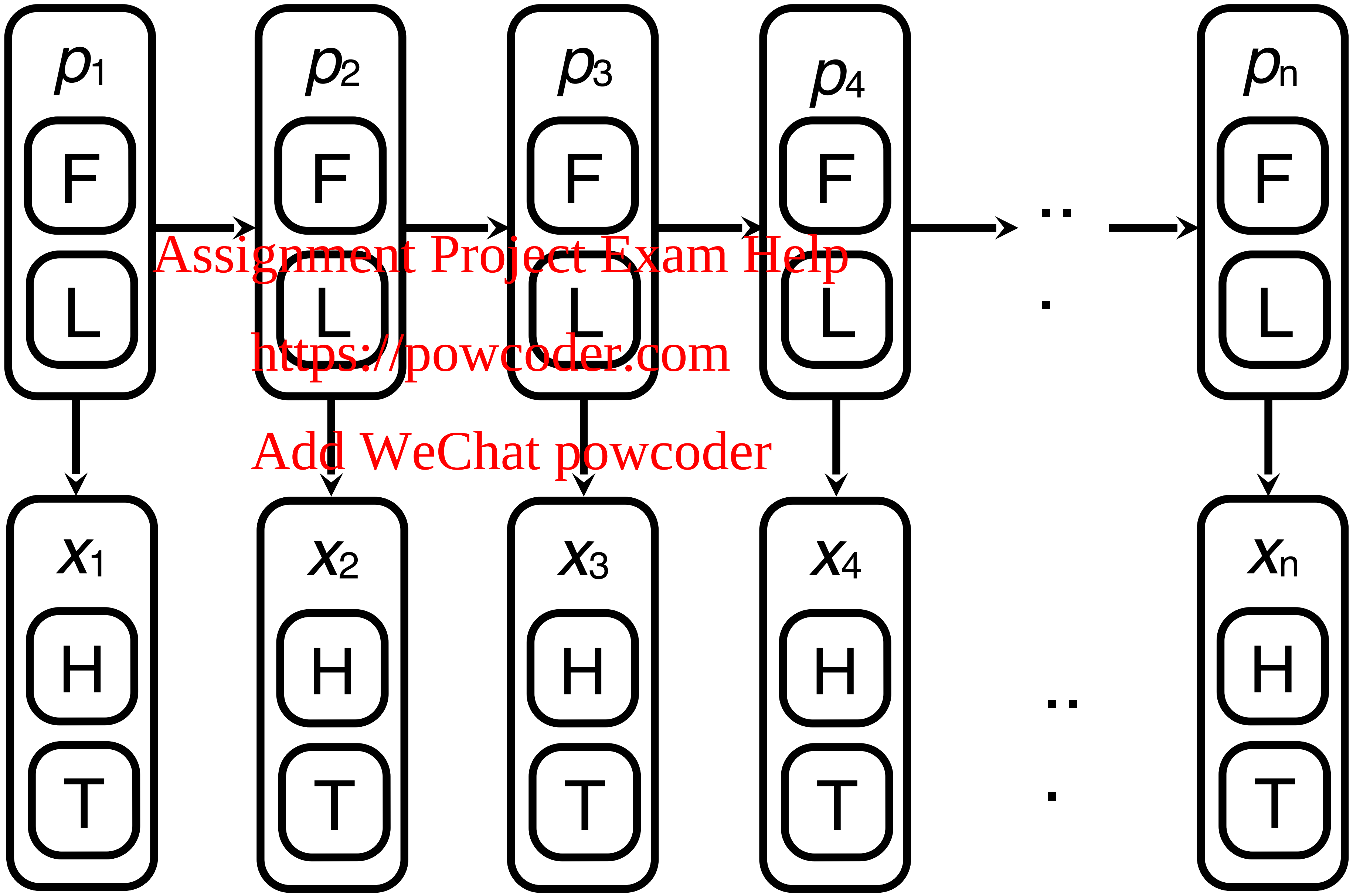
Hidden Markov Model

States encode which coin is used

F = fair
L = loaded

Emissions encode flip outcomes

H = heads
T = tails



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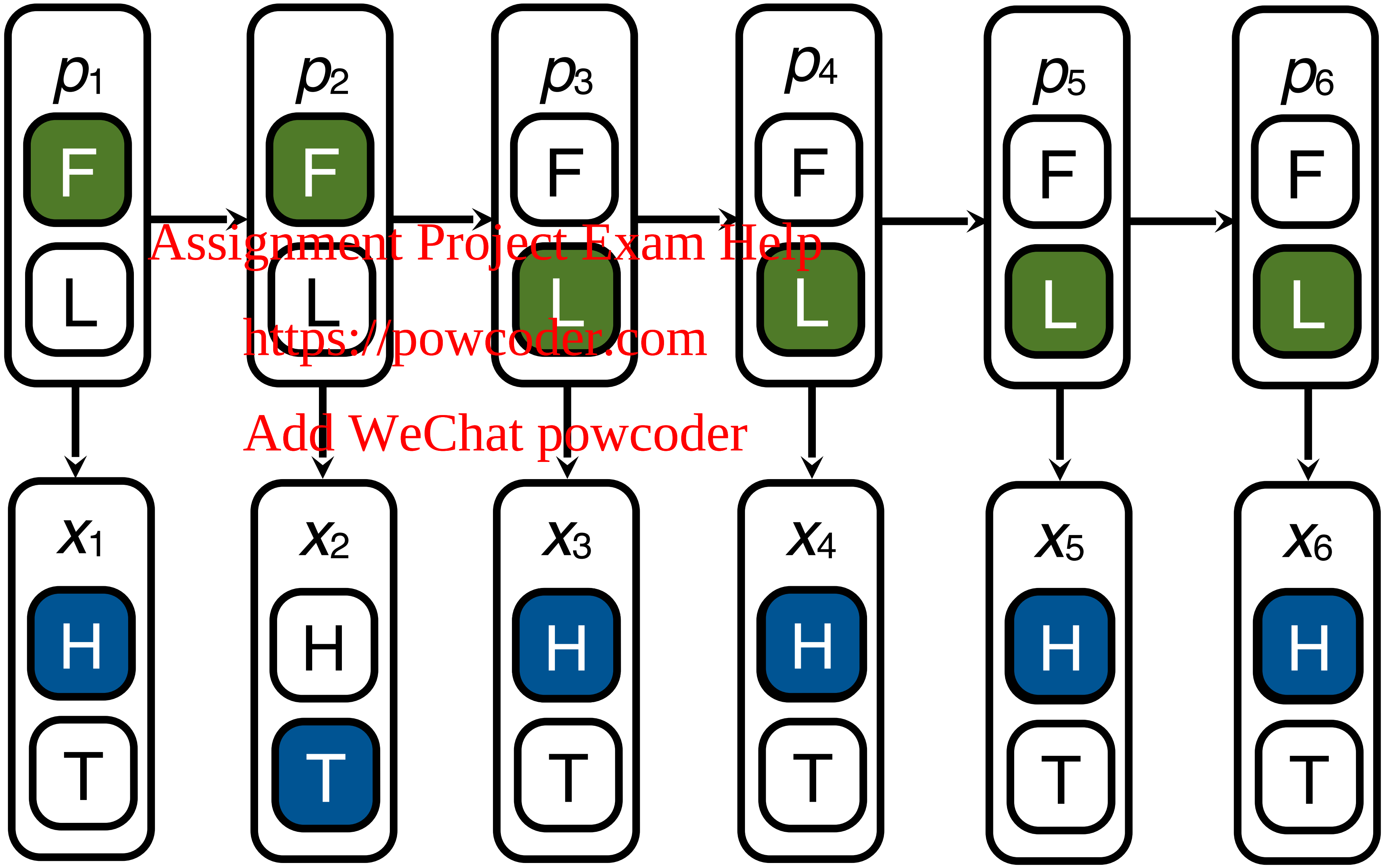
Hidden Markov Model

Example with six coin flips:

p = FFLLLL



x = HTHHHH

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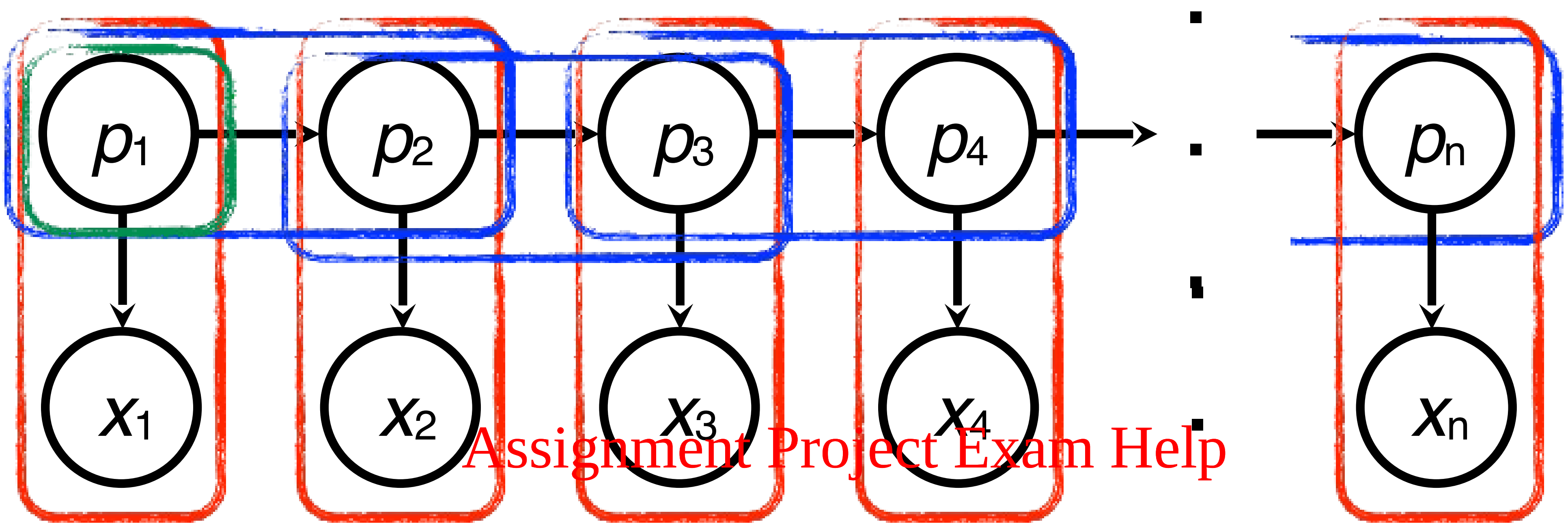
Hidden Markov Model



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$P(p_1, p_2, \ldots, p_n, x_1, x_2, \ldots, x_n) = ?$

$$P(p_1, p_2, \ldots, p_n, x_1, x_2, \ldots, x_n) = \prod_{k=1}^{n} P(x_k \mid p_k) \prod_{k=2}^{n} P(p_k \mid p_{k-1})\, P(p_1)$$

$|Q| \times |\Sigma|$ emission matrix E encodes $P(x_i \mid p_i)$ $E[p_i, x_i] = P(x_i \mid p_i)$

$|Q| \times |Q|$ transition matrix A encodes $P(p_i \mid p_{i-1})$ $A[p_{i-1}, p_i] = P(p_i \mid p_{i-1})$

$|Q|$ array I encodes initial probabilities of each state $I[p_i] = P(p_1)$

Q: the state set. Σ : the symbol set

Hidden Markov Model

Dealer repeatedly flips a coin. Coin is sometimes *fair*, with P(heads) = 0.5, sometimes *loaded*, with P(heads) = 0.8. Dealer occasionally switches coins, invisibly to you.

After each flip, dealer switches coins with probability 0.4

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A: transition

	F	L
F	0.6	0.4
L	0.4	0.6

E: emission

	H	T
F	0.5	0.5
L	0.8	0.2

| Q | × | ∑ | emission matrix *E* encodes $P(x_i \mid p_i)$ $\quad E[p_i, x_i] = P(x_i \mid p_i)$

| Q | × | Q | transition matrix *A* encodes $P(p_i \mid p_{i-1})$ $\quad A[p_{i-1}, p_i] = P(p_i \mid p_{i-1})$

Hidden Markov Model

A	F	L
F	0.6	0.4
L	0.4	0.6

E	H	T
F	0.5	0.5
L	0.8	0.2

Given A & E (right), what is the joint probability of p & x?

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p	F	F	F	L	L	L	F	F	F	F	F
x	T	H	T	H	H	H	T	H	T	T	H
P(x_i | p_i)	0.5	0.5	0.5	0.8	0.8	0.8	0.5	0.5	0.5	0.5	0.5
P(p_i | p_{i-1})	-	0.6	0.6	0.4	0.6	0.6	0.4	0.6	0.6	0.6	0.6

If P(p_1 = F) = 0.5, then joint probability = $0.5^9\ 0.8^3\ 0.6^8\ 0.4^2$

= 0.0000026874

Hidden Markov Model

Given flips, can we say when the dealer was using the loaded coin? How many different paths can generate X?

X =

T	**H**	**T**	**H**	**H**	**H**	**T**	**H**	**T**	**T**	**H**

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We want to find p^*, the most likely path given the emissions.

$$p^* = \underset{p}{\operatorname{argmax}} \, P(\, p \mid x \,) = \underset{p}{\operatorname{argmax}} \, P(\, p, x \,)$$

How to find p*? How many different state path p can produce x?

This is *decoding*. *Viterbi* is a common decoding algorithm.

Viterbi (from Wikipedia)

Andrew Viterbi

From Wikipedia, the free encyclopedia

Andrew James Viterbi (born Andrea Giacomo Viterbi; March 9, 1935) is an American electrical engineer and businessman who co-founded Qualcomm Inc. and invented the Viterbi algorithm. He is currently Presidential Chair Professor of Electrical Engineering at the University of Southern California's Viterbi School of Engineering, which was named in his honor in 2004 in recognition of his $52 million gift.

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Contents [hide]

Viterbi School of Engineering, west wall

Andrew J. Viterbi[1]

Born	Andrea Giacomo Viterbi March 9, 1935 (age 85) Bergamo, Italy
Citizenship	American

Early life [edit]

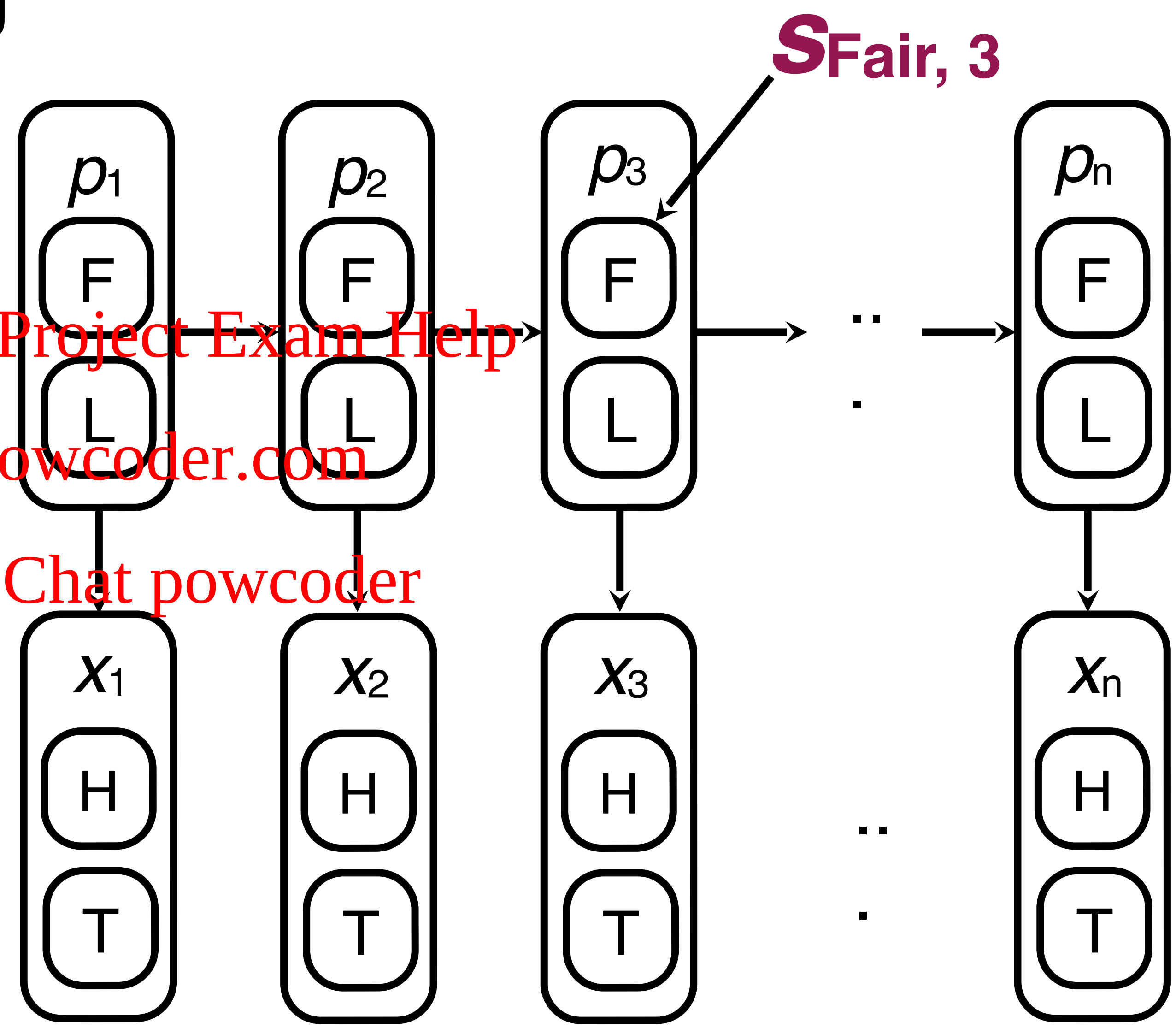
Viterbi was born to Italian Jewish family[2] in Bergamo, Italy and emigrated with them to the United States two years before World War II. His original name was Andrea, but when he was naturalized in the US, his parents anglicized it to Andrew.

Hidden Markov Model: Viterbi algorithm

Bottom-up dynamic programming

$S_{k,\,i}$ = score/probability of the most likely path up to step i with p_i = k

Start at step 1, calculate successively longer $S_{k,\,i}$'s



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Question for you: use $S_{k,l}$ to represent the maximum probability of seeing x

Hidden Markov Model: Viterbi algorithm

Given transition matrix *A* and emission matrix *E* (right), what is the most probable path *p* for the following *x*?

Initial probabilities of F/L are 0.5 (no preference for fair or loaded coin)

A	F	L
F	0.6	0.4
L	0.4	0.6

E	H	T
F	0.5	0.5
L	0.8	0.2

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p	?	?	?	?	?	?	?	?	?	?	?
x	T	H	T	H	H	H	T	H	T	T	H
$s_{\text{Fair}, i}$	0.25	?	?	?	?	?	?	?	?	?	?
$s_{\text{Loaded}, i}$	0.1	?	?	?	?	?	?	?	?	?	?

$S_{\text{Fair},1}$=0.5*0.5

$S_{\text{Loaded},1}$=0.5*0.2

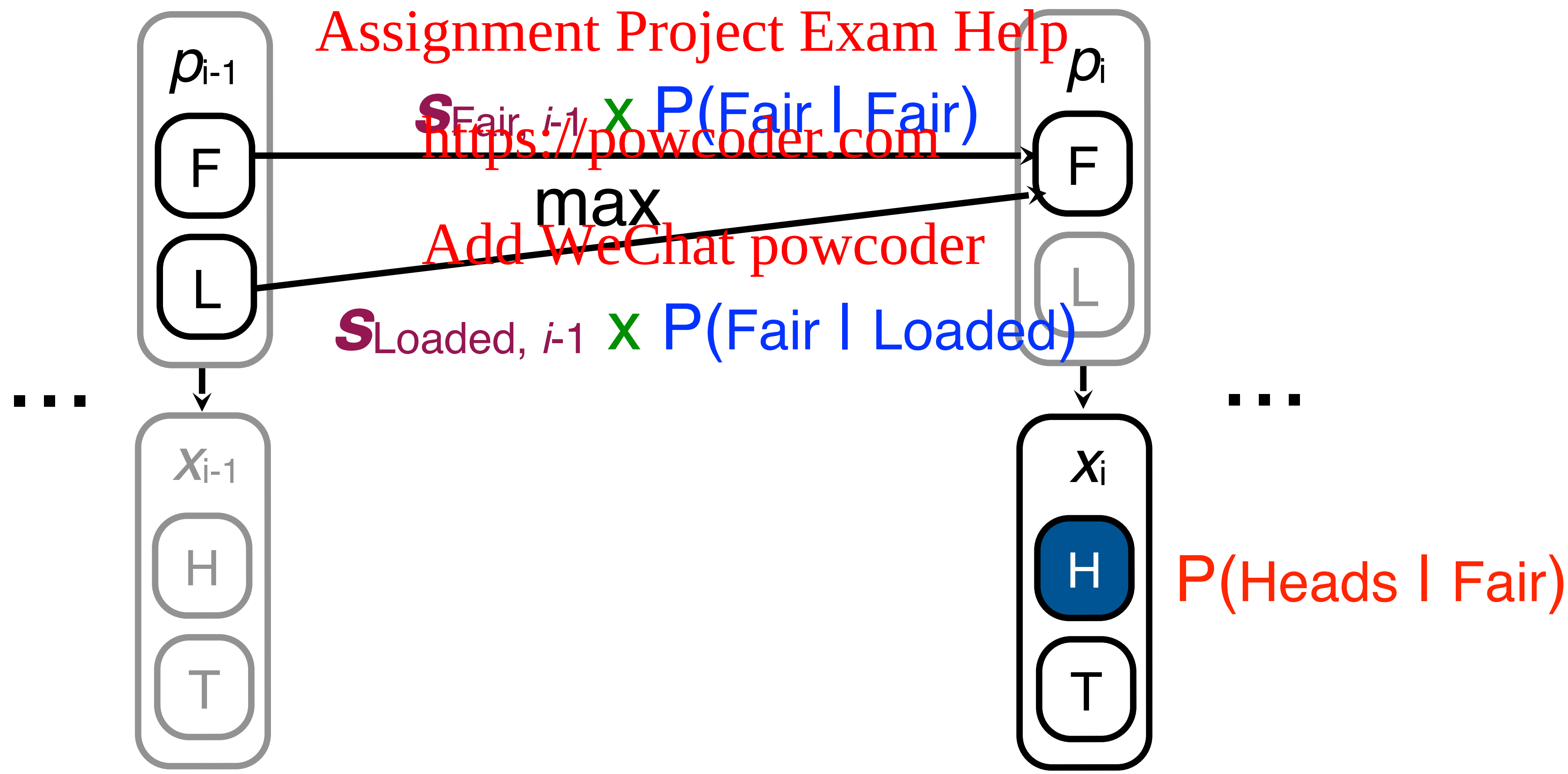
Viterbi fills in all the question marks

Hidden Markov Model: Viterbi algorithm

$$s_{Fair,i} = P(\text{Heads} \mid \text{Fair}) \times \max_{k \in \{\text{Fair, Loaded}\}} \{ s_{k,i-1} \times P(\text{Fair} \mid k) \}$$

Emission prob

Transition prob



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$s_{k,i}$ = score/probability of the most likely path up to step i with $p_i = k$

Hidden Markov Model: Viterbi algorithm

	Step 1	Step 2	Step 3	Step 4 ...
x	T	H	T	H
$S_{F,\,i}$	$p(T\mid F) = 0.5$ $p(F) = 0.5$ $S_{F,\,1} = 0.5^2$	$p(H\mid F) = 0.5$ max: $p(F\mid F) = 0.6$ $0.5^3 \cdot 0.6$ $p(F\mid L) = 0.4$ $0.2 \cdot 0.4 \cdot 0.5^2$ F wins max $S_{F,\,2} = 0.5^3 \cdot 0.6$	$p(T\mid F) = 0.5$ max: $p(F\mid F) = 0.6$ $0.5^4 \cdot 0.6^2$ $p(F\mid L) = 0.4$ $0.4 \cdot 0.4 \cdot 0.5^2 \cdot 0.8 \cdot 0.5$ F wins max $S_{F,3} = 0.5^4 \cdot 0.6^2$	etc
$S_{L,\,i}$	$p(T\mid L) = 0.2$ $p(L) = 0.5$ $S_{L,\,1} = 0.2 \cdot 0.5$	$p(H\mid L) = 0.8$ max: $p(L\mid F) = 0.4$ $0.4 \cdot 0.5^2 \cdot 0.8$ $p(L\mid L) = 0.6$ $0.2 \cdot 0.5 \cdot 0.6 \cdot 0.8$ F wins max $S_{L,\,2} = 0.4 \cdot 0.5^2 \cdot 0.8$	etc	etc

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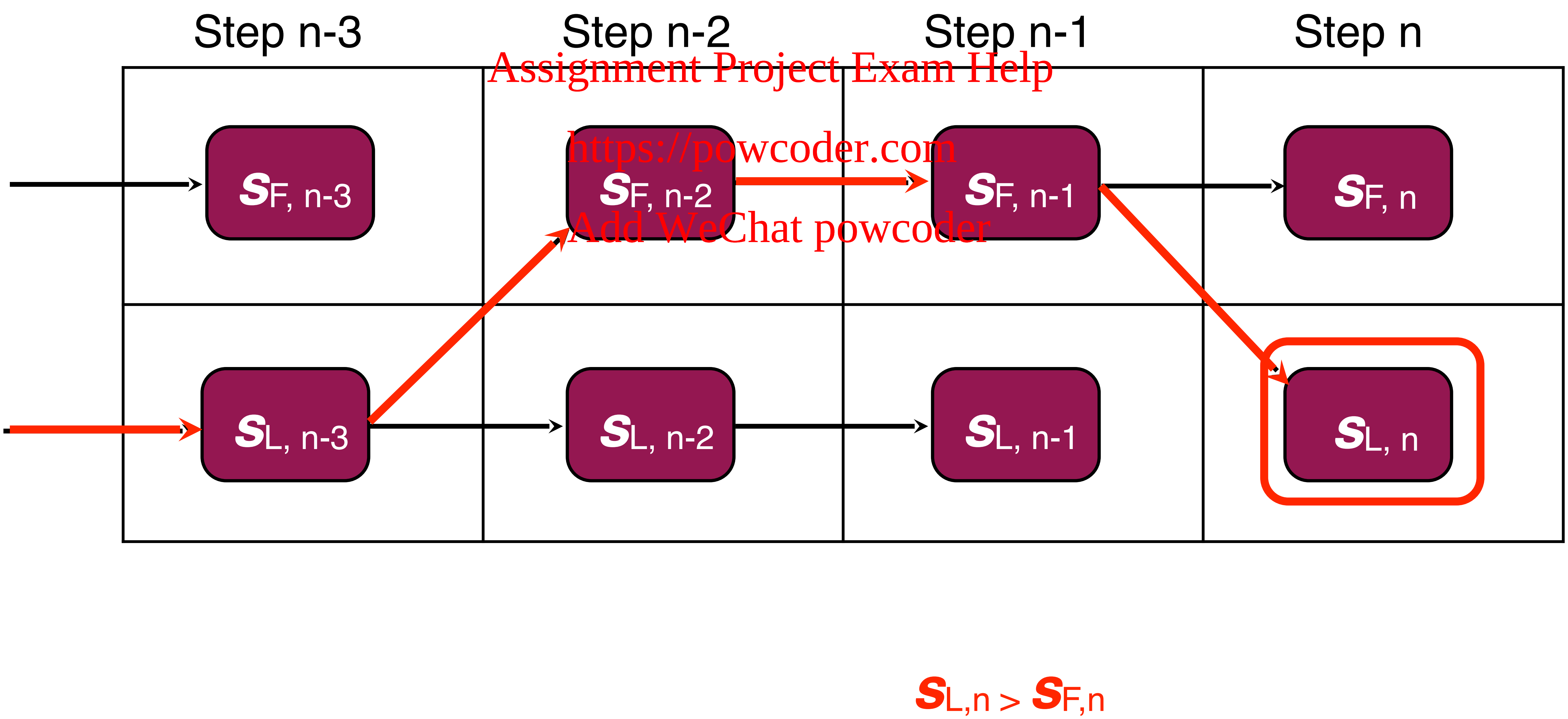
Hidden Markov Model: Viterbi algorithm

Pick state in step *n* with highest score; *backtrace* for most likely path

Backtrace according to which state *k* “won” the max in:



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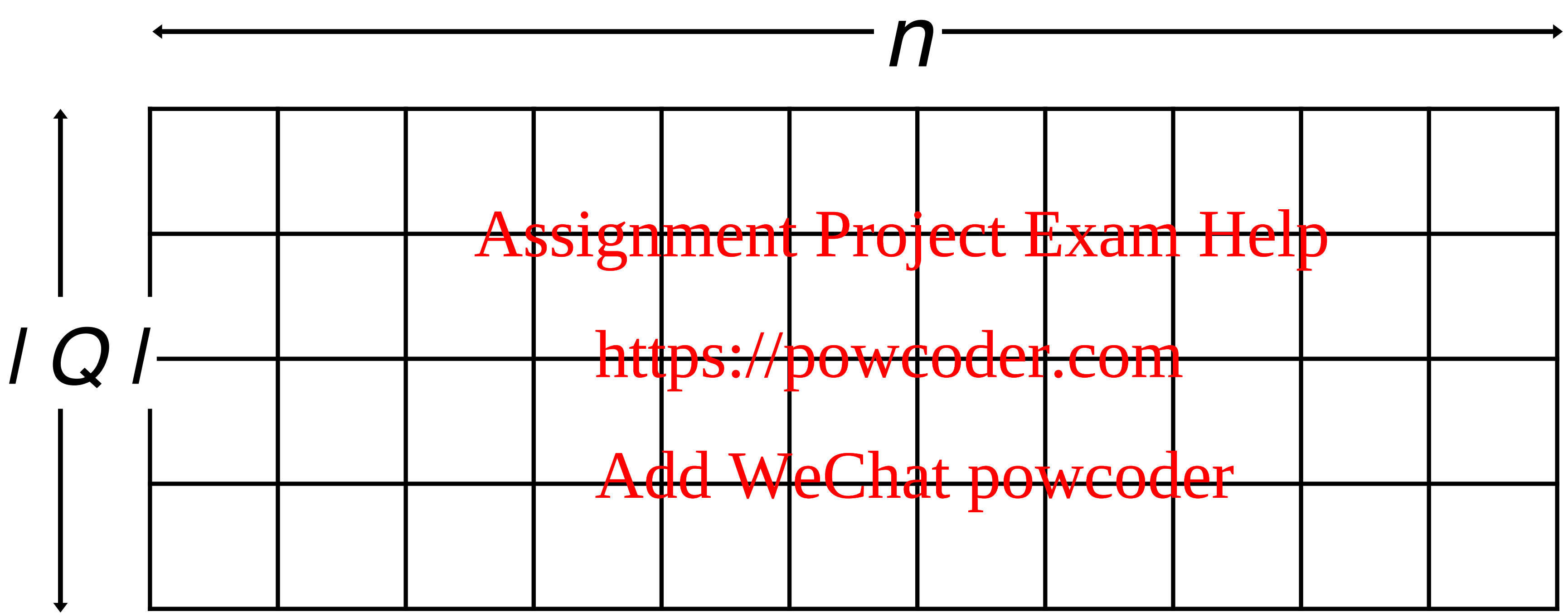
Hidden Markov Model: Viterbi algorithm

How much work did we do, given *Q* is the set of states and *n* is the length of the sequence?



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$\# \, s_{k,i}$ values to calculate = $n \cdot |Q|$, each involves max over $|Q|$ products

$O(n \cdot |Q|^2)$

Matrix A has $|Q|^2$ elements, E has $|Q||\Sigma|$ elements, I has $|Q|$ elements

Hidden Markov Model: Viterbi algorithm

```
>>> hmm = HMM({"FF":0.6, "FL":0.4, "LF":0.4,
"LL":0.6},
...           {"FH":0.5, "FT":0.5, "LH":0.8,
"LT":0.2},
...           {"F":0.5, "L":0.5})
>>> prob, _ = hmm.viterbi("THTHHHTHTTH")
>>> print prob
2.86654464e-06
>>> prob, _ = hmm.viterbi("THTHHHTHTTH" * 100)
>>> print prob
0.0
```

Occasionally dishonest casino setup

Repeat string 100 times

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What happened? Underflow!

Hidden Markov Model: Viterbi algorithm

```
>>> hmm = HMM({"FF":0.6, "FL":0.4, "LF":0.4, "LL":0.6},
...           {"FH":0.5, "FT":0.5, "LH":0.8, "LT":0.2},
...           {"F":0.5, "L":0.5})
>>> prob, _ = hmm.viterbi("THTHHHTHTTH")
>>> print prob
2.86654464e-06
>>> prob, _ = hmm.viterbi("THTHHHTHTTH" * 100)
>>> print prob
0.0
>>> logprob, _ = hmm.viterbiL("THTHHHTHTTH" * 100)
>>> print logprob
-1824.4030071946879
```

Repeat string 100 times

log-space Viterbi

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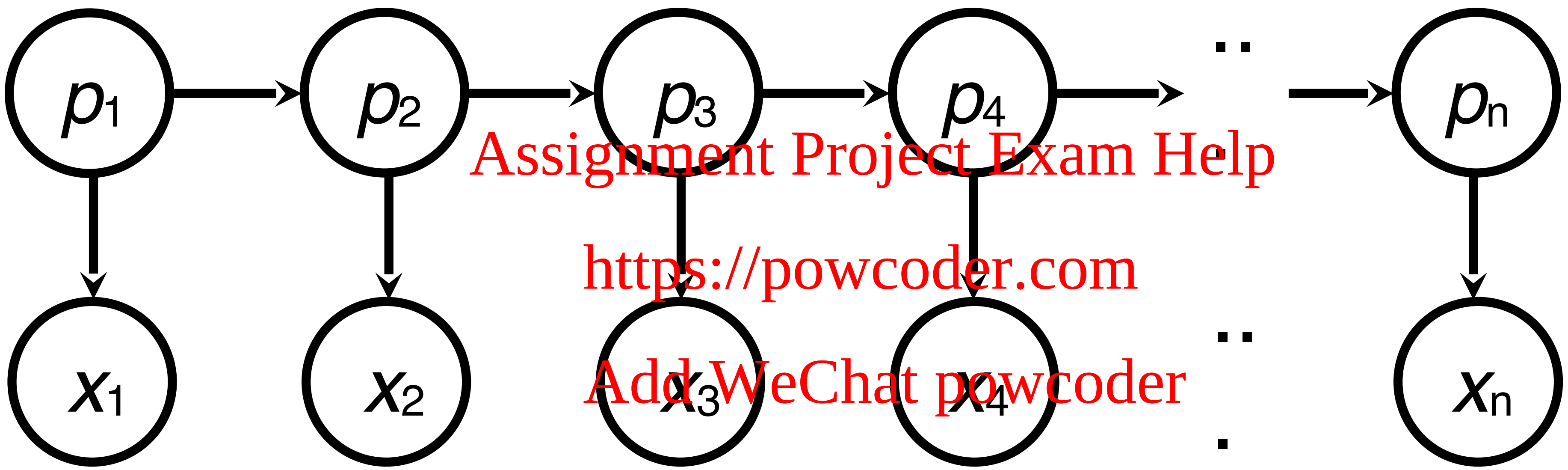
When multiplying many numbers in (0, 1], we quickly approach the smallest number representable in a machine word. Past that we have *underflow* and processor rounds down to 0.

Switch to log space. Multiplies become adds.

Hidden Markov Model

Task: design an HMM for finding CpG islands?



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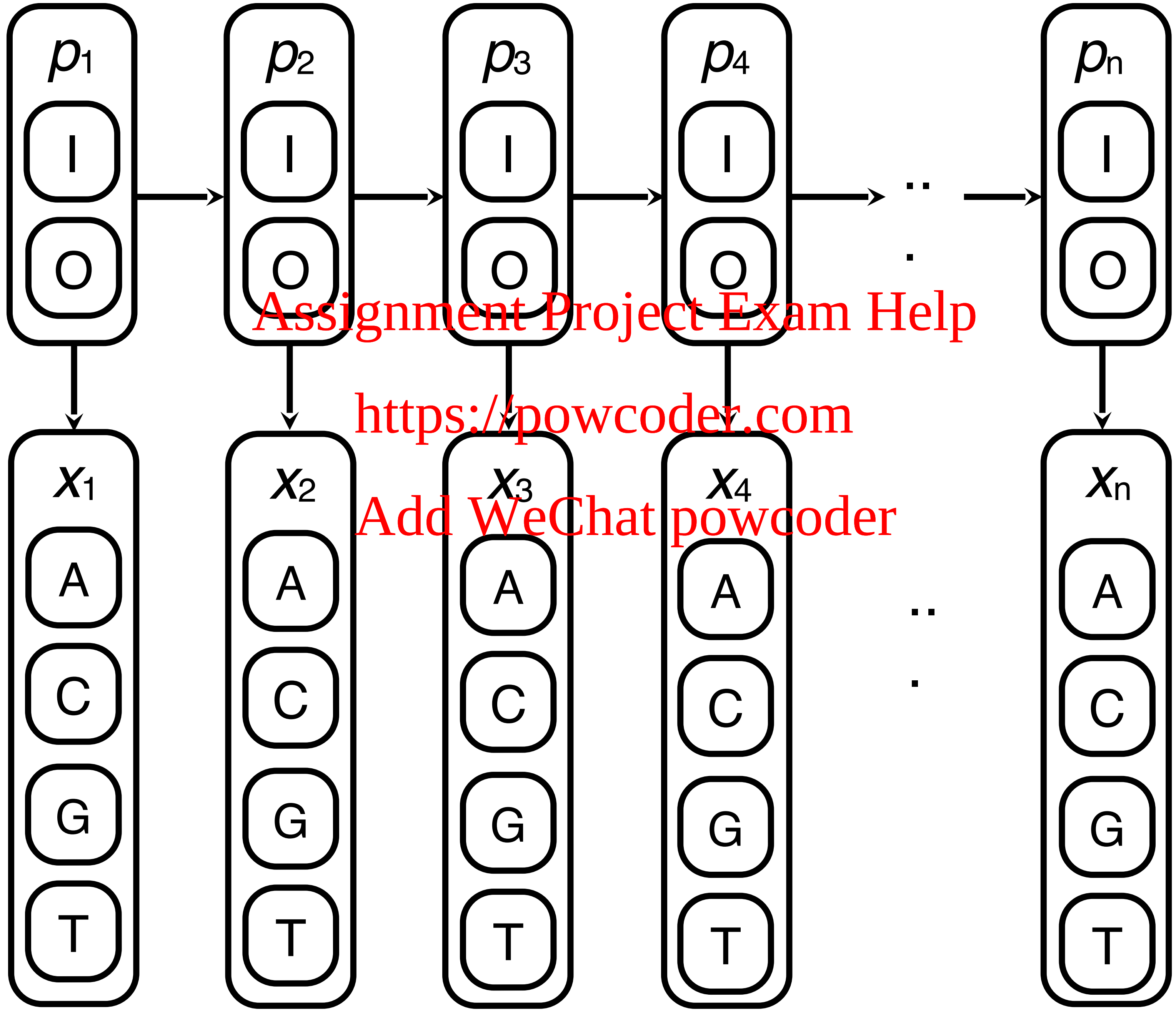
Hidden Markov Model

Idea 1: Q = { inside, outside }, $\sum$ = { A, C, G, T }



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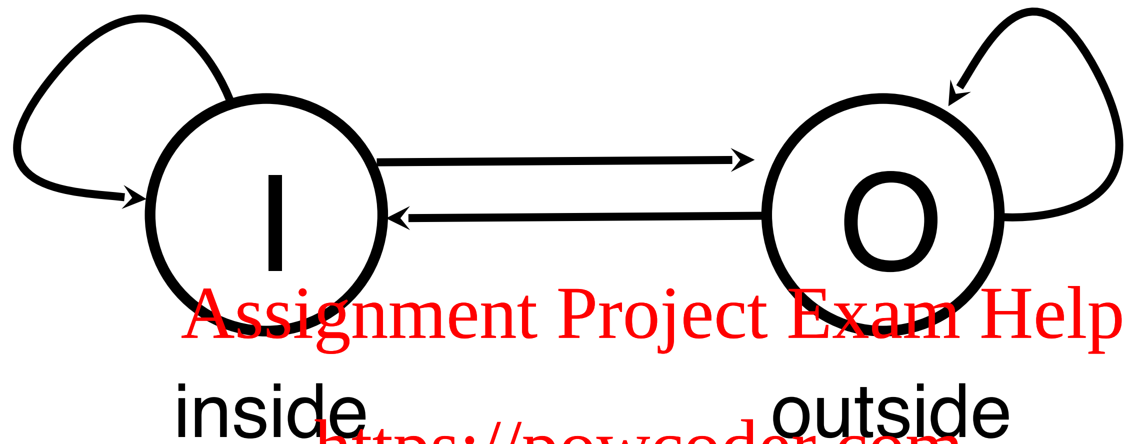
Hidden Markov Model

Idea 1: $Q = \{$ inside, outside $\}$, $\Sigma = \{$ A, C, G, T $\}$



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A	I	O
I		
O		

Transition matrix

E	A	C	G	T
I				
O				

Emission matrix

Estimate as fraction of positions where we transition from inside to outside

Estimate as fraction of nucleotides inside islands that are C

Hidden Markov Model

Example 1 using HMM idea 1:

A	I	O
I	0.8	0.2
O	0.2	0.8

E	A	C	G	T
I	0.1	0.4	0.4	0.1
O	0.25	0.25	0.25	0.25

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x: ATATATACGCGCGCGCGCGCGATATATATATATA

p: OOOOOOOIIIIIIIIIIIIIIOOOOOOOOOOOOO

(from Viterbi)

Hidden Markov Model

Example 2 using HMM idea 1:

A	I	O
I	0.8	0.2
O	0.2	0.8

E	A	C	G	T
I	0.1	0.4	0.4	0.1
O	0.25	0.25	0.25	0.25

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x: ATATCGCGCGCGATATATCGCGCGCGATATATAT

π: OOOOIIIIIIIIOOOOOOIIIIIIIIOOOOOOOO

(from Viterbi)

Hidden Markov Model

Example 3 using HMM idea 1:

A	I	O
I	0.8	0.2
O	0.2	0.8

E	A	C	G	T
I	0.1	0.4	0.4	0.1
O	0.25	0.25	0.25	0.25

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x: ATATATACCCCCCCCCCCCCCATATATATATATA

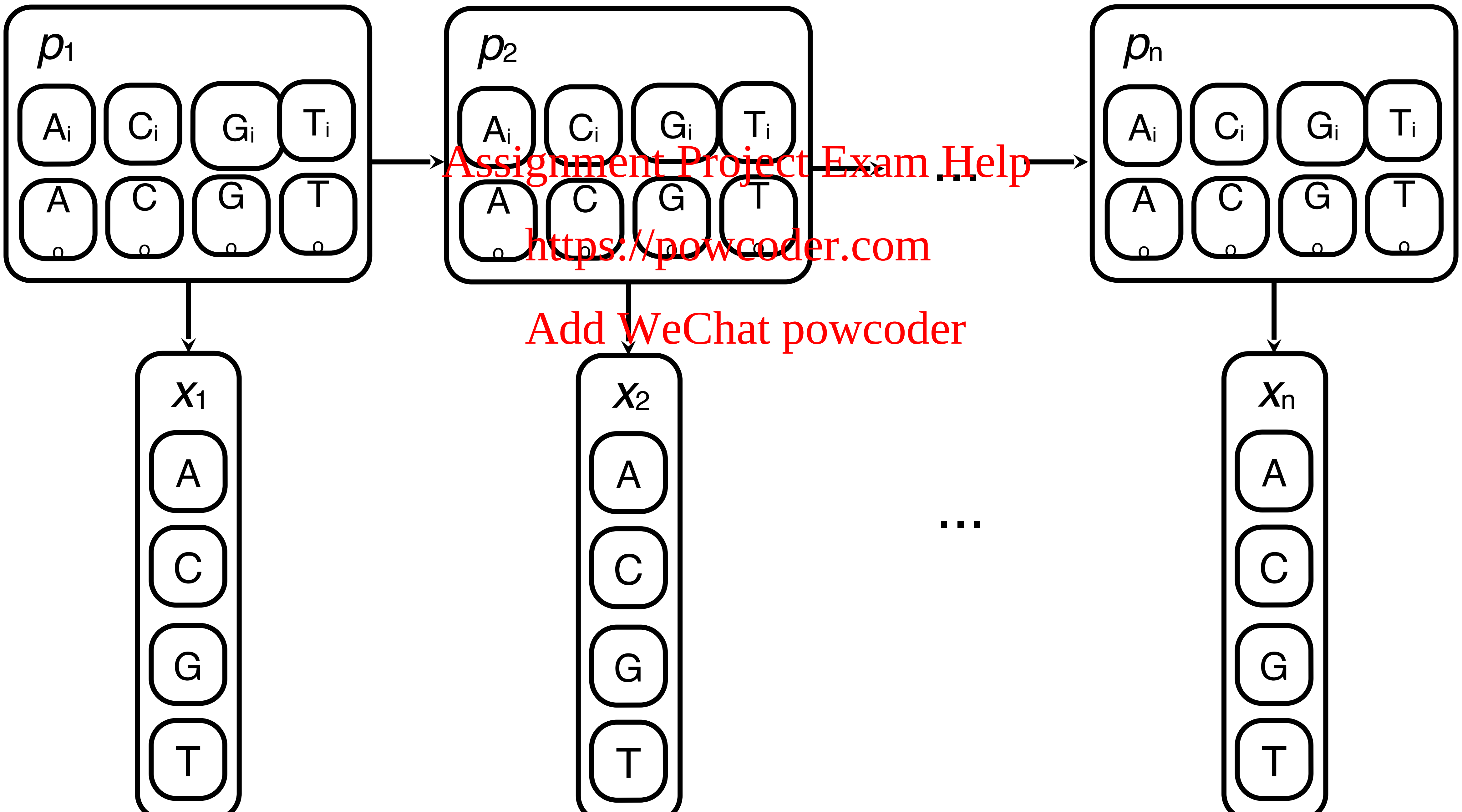
p: OOOOOOOIIIIIIIIIIIIIIOOOOOOOOOOOOO

(from Viterbi)

Oops - not a CpG island!

Hidden Markov Model

Idea 2: $Q = \{ A_i, C_i, G_i, T_i, A_o, C_o, G_o, T_o \}$, $\Sigma = \{ A, C, G, T \}$



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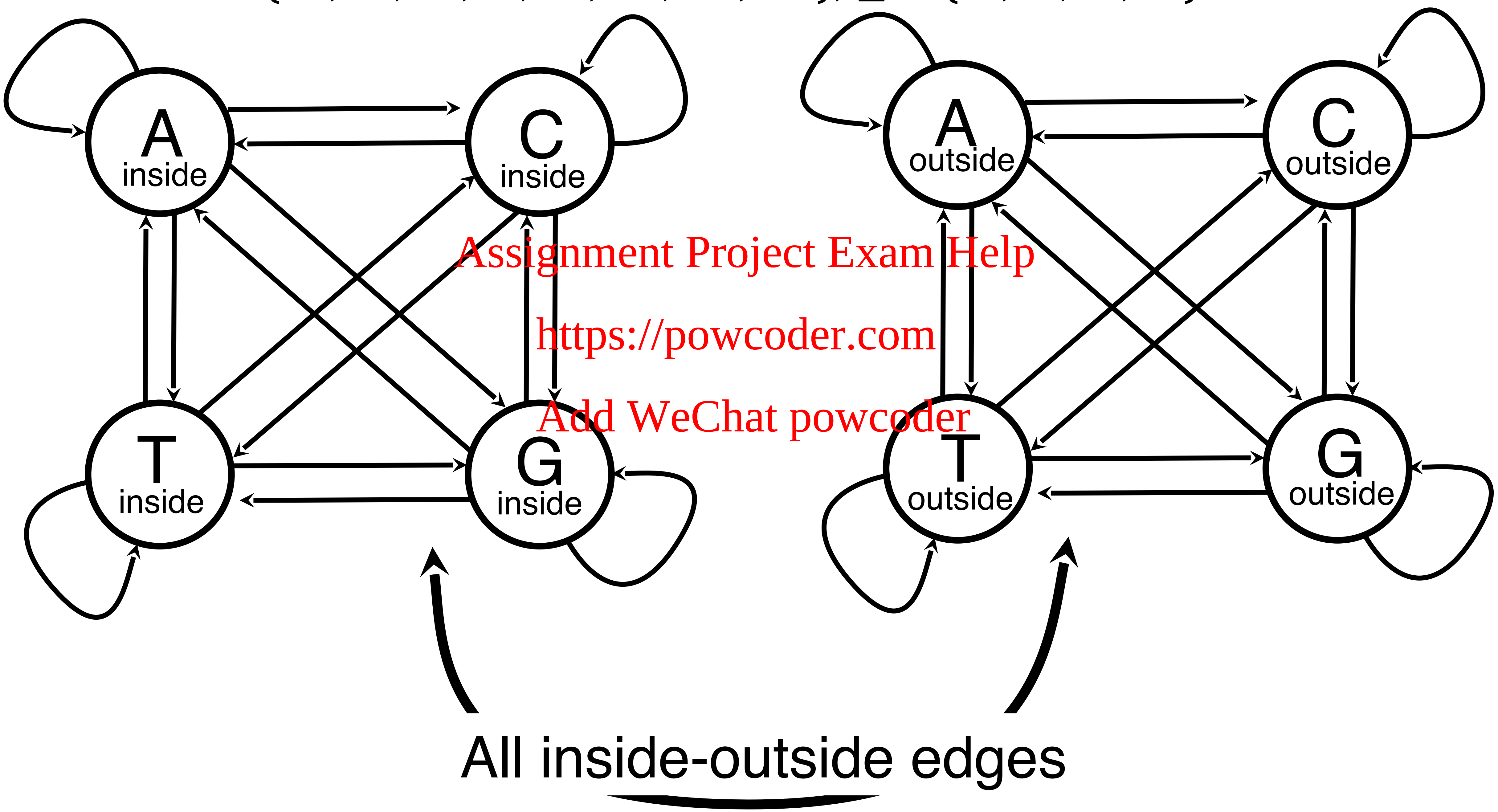
Hidden Markov Model

Idea 2: $Q = \{ A_i, C_i, G_i, T_i, A_o, C_o, G_o, T_o \}$, $\Sigma = \{ A, C, G, T \}$



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Hidden Markov Model

Idea 2: $Q = \{ A_i, C_i, G_i, T_i, A_o, C_o, G_o, T_o \}$, $\Sigma = \{ A, C, G, T \}$

A	A_i	C_i	G_i	T_i	A_o	C_o	G_o	T_o
A_i								
C_i								
G_i								
T_i								
A_o								
C_o								
G_o								
T_o								

Estimate $P(C_i \mid T_i)$ as fraction of all dinucleotides where first is an inside T, second is an inside C

E	A	C	G	T
A_i	1	0	0	0
C_i	0	1	0	0
G_i	0	0	1	0
T_i	0	0	0	1
A_o	1	0	0	0
C_o	0	1	0	0
G_o	0	0	1	0
T_o	0	0	0	1

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```
[[  1.85152516e-01   2.75974026e-01   4.00289017e-01
1.37026750e-01
    3.19045117e-04   3.19045117e-04   6.38090233e-04
2.81510397e-04]
 [  1.89303979e-01   3.58523577e-01   2.52868527e-01
1.97836007e-01
    4.28792308e-04   5.72766368e-04   3.75584503e-05
4.28792308e-04]
 [  1.72369088e-01   3.29501650e-01   3.55446538e-01
1.40829292e-01
    3.39848138e-04   4.94038497e-04   7.64658311e-04
2.54886104e-04]
 [  9.38783432e-02   3.40823149e-01   3.75970400e-01
1.86949063e-01
    2.56686367e-04   5.57197235e-04   1.05804868e-03
5.07112091e-04]
 [  0.00000000e+00   3.78291020e-05   0.00000000e+00
0.00000000e+00
    2.94813496e-01   1.94641138e-01   2.86962055e-01
2.23545482e-01]
 [  0.00000000e+00   7.57154865e-05   0.00000000e+00
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    3.26811872e-01   2.94079570e-01   6.17258712e-02
3.17306971e-01]
 [  0.00000000e+00   5.73810399e-05   0.00000000e+00
0.00000000e+00
    2.57133507e-01   2.33483327e-01   2.94234944e-01
2.15090841e-01]
 [  0.00000000e+00   3.11417347e-05   0.00000000e+00
```

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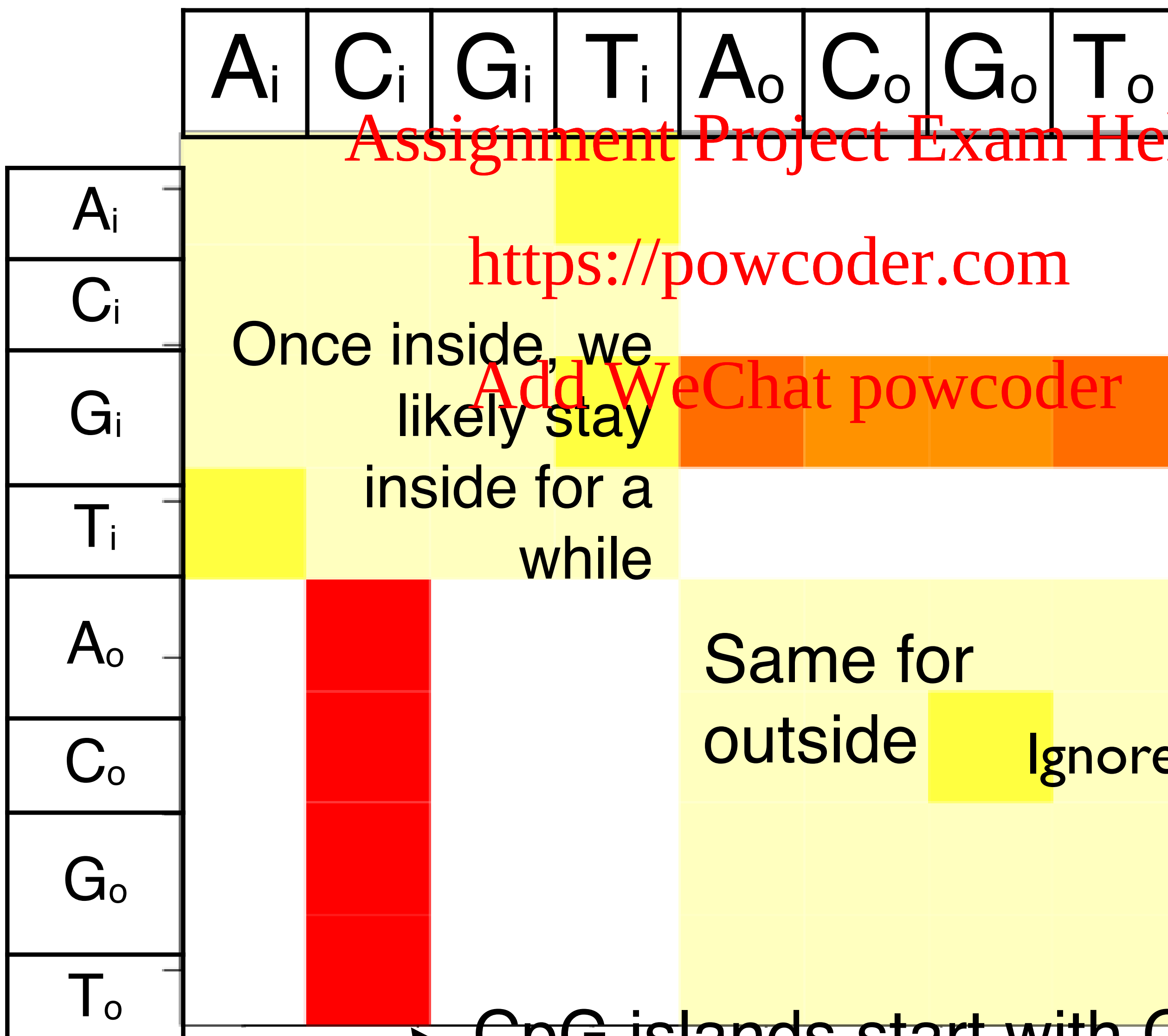
Hidden Markov Model

Actual trained transition matrix A:

Red & orange: low probability

Yellow: high probability

White: probability = 0



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CpG islands end with G (in fact, they end with CG)

Ignore the small yellow blocks

CpG islands start with C (in fact, they start with CG)

Hidden Markov Model

Viterbi result; lowercase = *outside*, uppercase = *inside*:

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Hidden Markov Model

Viterbi result: lowercase = *outside*, uppercase = *inside*:

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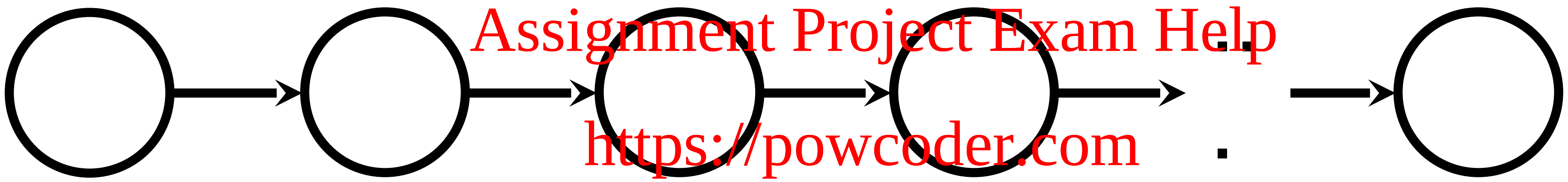
Hidden Markov Model

Many of the Markov chains and HMMs we've discussed are *first order,* but we can also design models of higher orders

First-order Markov chain:



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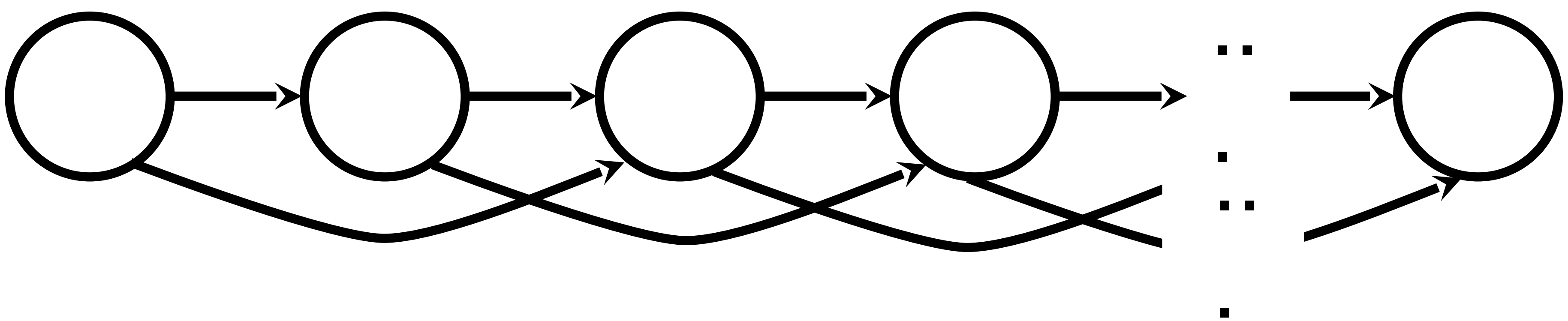
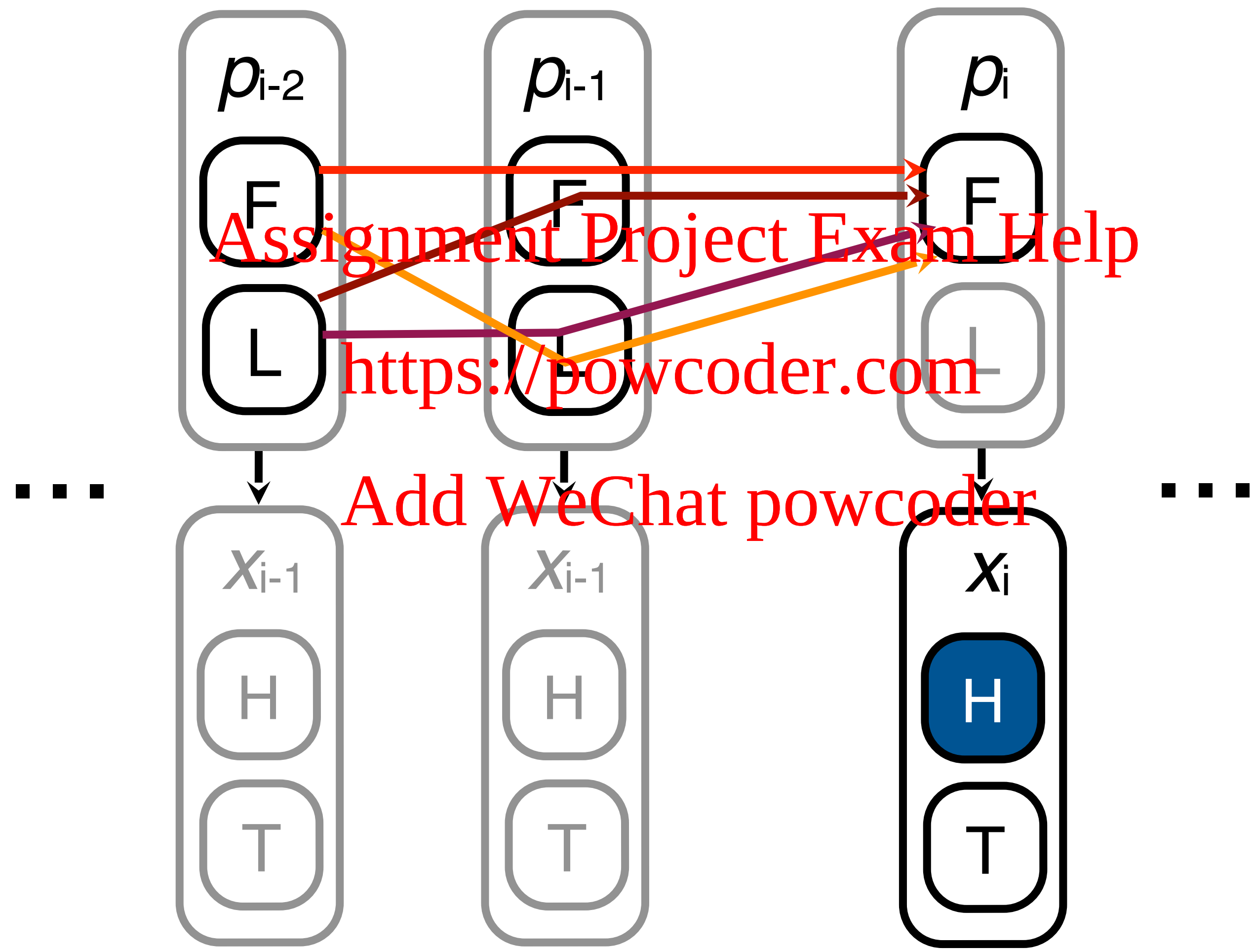
Second-order Markov chain:



Hidden Markov Model

For higher-order HMMs, Viterbi $s_{k,\,i}$ no longer depends on just the previous state assignment



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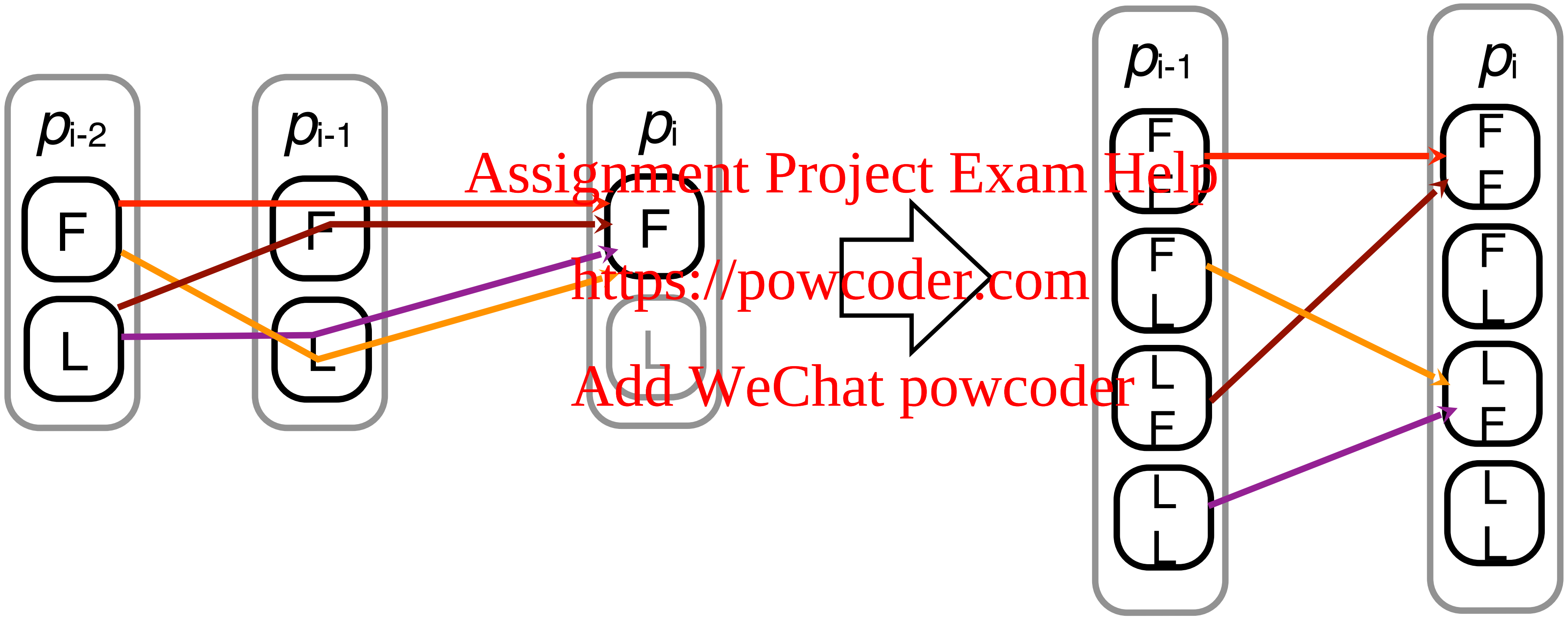
Can sidestep the issue by expanding the state space...

Hidden Markov Model

Now *one* state encodes the last *two* “loadedness”es of the coin



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$Q = \{\ F, L\ \}$ $\qquad$ $Q = \{\ F, L\ \} \times \{\ F, L\ \}$

After expanding, usual Viterbi works fine.