Neuromechanics of Human Motion

Bayesian Statistics

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Recap — Illusions, Perception, Bayes

1. Priors
2. Adaptation
3. Sensory Noise
4. Multisensory Integration
5. Bayes

Recap — Bayes Theorem

$$p(A|B) = \frac{p(B|A) \cdot p(A)}{p(B)}$$

- conditional probability
- account for priors, adaptation, multisensory illusions

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$$p(A|B) = \frac{p(B|A) \cdot p(A)}{p(B|A) \cdot p(A) + p(B|A') \cdot p(A')}$$

- point probabilities
- see last lecture

Lecture Objectives — Bayes Theorem

1. Go over point estimate example in class
2. Quatify influence of priors, adaptation
3. Extend to continuous probability
4. Go over continuous example in class
5. Multisensory integration

Point Probabilities

Why Bayesian?

Powerful way to account for new evidence given **prior** beliefs

$$p(A|B) = \frac{p(B|A) \cdot p(A)}{p(B)}$$

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x Likelihood
(new evidence)

Prior

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$p(B)$ = probability of B

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x Likelihood
(new evidence)

Prior

Posterior

p(B) = marginal probability (e.g., true *positive* & false *positive* tests)

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$$p(A|B) = \frac{p(B|A) \cdot p(A)}{p(B|A) \cdot p(A) + p(B|A') \cdot p(A')}$$

x Likelihood
(new evidence)

Prior

Posterior

p(B) = marginal probability (e.g., true *positive* & false *positive* tests)
classic example: A = preg, A' = not preg, B = + test, B' = - test


Old station fights time

Point Estimate Example

Let us say we have a monkey opening and closing its hand, while we record from its primary motor cortex. To build an effective brain machine interface (e.g., prosthetic), we want to decode if the monkey's hand is open or closed by observing whether a neuron spikes or not.

1. Some neurons fire to move the hand or just fire spontaneously. Lets assume our initial, prior guess on whether the monkey's hand is open is 40%, p(open) = 0.4.
2. The probability of observing a spike given an open hand is recorded is 75%, $p(spike|open) = 0.75$.
3. The probability of observing a spike given a closed hand (sometimes neurons fire spontaneously): $p(spike|closed) = 0.25$.
4. We observe a spike. What is the probability that the hand is open, $p(open|spike)$?

Point Estimate Example

$$p(open|spike) = \frac{p(spike|open) \cdot p(open)}{p(spike|open) \cdot p(open) + p(spike|closed) \cdot p(closed)}$$

Knowns:

$p(open) = 0.4$

$p(spike|open) = 0.75$

$p(spike|closed) = 0.25$

Unknowns:

$p(closed) =?$

$p(open|spike) =?$

Point Estimate Example

$$p(open|spike) = \frac{p(spike|open) \cdot p(open)}{p(spike|open) \cdot p(open) + p(spike|closed) \cdot p(closed)}$$

Knowns:

$p(open) = 0.4$

$p(spike|open) = 0.75$

$p(spike|closed) = 0.25$

Unknowns:

$p(closed) = 1 - p(open) = 0.6$

$p(open|spike) = ?$

Point Estimate Example

$$p(open|spike) = \frac{p(spike|open) \cdot p(open)}{p(spike|open) \cdot p(open) + p(spike|closed) \cdot p(closed)}$$

Knowns:

$p(open) = 0.4$

$p(spike|open) = 0.75$

$p(spike|closed) = 0.25$

Unknowns:

$p(closed) = 1 - p(open) = 0.6$

$p(open|spike) = 0.67$

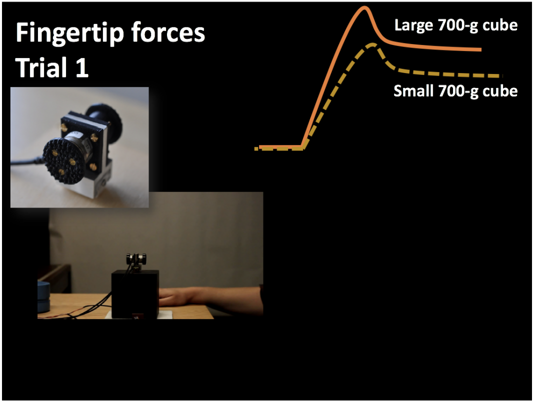
$$p(open|spike) = 0.67 = \frac{0.75 \cdot 0.4}{0.75 \cdot 0.4 + 0.25 \cdot 0.6}$$

Influence of our PRIOR beliefs

How much of our prediction is influenced by our prior belief that the hand is open or not?

prior	posterior
0.1	0.25
0.2	0.43
0.3	0.56
0.4	0.67
0.5	0.75
0.6	0.82
0.7	0.88
0.8	0.92
0.9	0.96

Size Weight Illusion



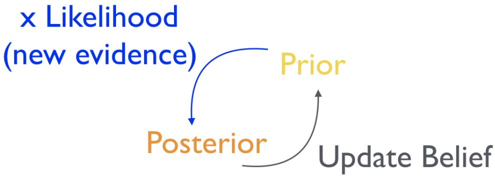
Mismatch, despite same weight

Bayes' Theorem can capture PRIOR beliefs

Why Bayesian?

Powerful way to **continually** account for new evidence given prior beliefs

$$p(A|B) = \frac{p(B|A) \cdot p(A)}{p(B)}$$



$p(A|B)$ **becomes** $p(A)$ **on the next iteration!**

Point Estimate Example Continued

Let's go back to our previous example.

1. For our initial prior, $p(open) = 0.4$ (40% probability the hand was open).
2. We then calculated the posterior, $p(open|spike) = 0.67$ (67% probability that the hand was open given we observed a spike).
3. Our current best guess on the probability that the hand is open is 67%
4. Critically, we can keep iterating through this process to *continually* update our belief.
5. Lets say we observe another spike. Now, what is the probability the hand is open?

Point Estimate Example

$$p(open|spike) = \frac{p(spike|open) \cdot p(open)}{p(spike|open) \cdot p(open) + p(spike|closed) \cdot p(closed)}$$

Knowns:

$p(open) = 0.67$

$p(spike|open) = 0.75$

$p(spike|closed) = 0.25$

Unknowns:

$p(closed) = ?$

$p(open|spike) = ?$

Point Estimate Example

$$p(open|spike) = \frac{p(spike|open) \cdot p(open)}{p(spike|open) \cdot p(open) + p(spike|closed) \cdot p(closed)}$$

Knowns:

$p(open) = 0.67$

$p(spike|open) = 0.75$

$p(spike|closed) = 0.25$

Unknowns:

$p(closed) = 1 - p(open) = 0.33$

$p(open|spike) = ?$

Point Estimate Example

$$p(open|spike) = \frac{p(spike|open) \cdot p(open)}{p(spike|open) \cdot p(open) + p(spike|closed) \cdot p(closed)}$$

Knowns:

$p(open) = 0.67$

$p(spike|open) = 0.75$

$p(spike|closed) = 0.25$

Unknowns:

$p(closed) = 1 - p(open) = 0.33$

$p(open|spike) = 0.86$

$$p(open|spike) = 0.86 = \frac{0.75 \cdot 0.67}{0.75 \cdot 0.67 + 0.25 \cdot 0.33}$$

Point Estimate Example Continued

Let's keep going and pretend we observed 5 spikes in row from our initial belief of 40%. Calculating $p(open|spike)$ for each iteration leads to:

0.67

0.86

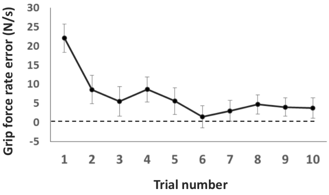
0.95

0.98

0.99

Adaptation

Grip/lift errors are rapidly corrected



Learning Curve

Bayes' Theorem can capture ADAPTATION

Continuous Probability Distributions

Continuous Probability Distributions

1. Analytical
   a. Normal Distribution
   b. Conjugate priors
2. Numerical
   a. Brute Force - Discretizing

Continuous Probability Distributions

1. Analytical
   a. Normal Distribution
   b. Conjugate priors
2. Numerical
   a. Brute Force - Discretizing
3. Noise in the Nervous System

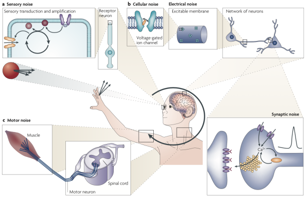
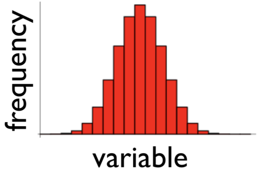


Figure 1 | **Overview of the behavioural loop and the stages at which noise is present in the nervous system.** **a** | Sources of sensory noise include the transduction of signals. This is exemplified here by a photoreceptor and its signal-amplification cascade. **b** | Sources of cellular noise include the ion channels of excitable membranes, synaptic transmission and network interactions (see BOX 2). **c** | Sources of motor noise include motor neurons and muscle. In the behavioural task shown (catching a ball), the nervous system has to act in the presence of noise in sensing, information processing and movement.

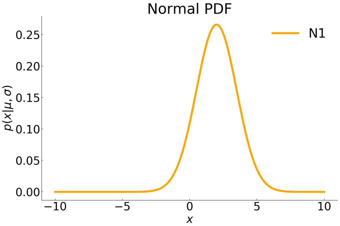
Analytical

Probability Distributions



1. Just a histogram
2. Describes the structure of randomness of some variable.
3. Area sums to 1.0 (100%)
4. Often, we can represent the structure of randomness with a small number of parameters

Normal Distribution



$$p(x|\mu,\sigma) = \frac{1}{\sigma\sqrt{2\pi}}\, e^{-\frac{(x-\mu)^2}{2\sigma^2}}$$

$$\mathcal{N}(\mu,\sigma^2)$$

Probability of a value x, given some known mean (μ) and standard deviation (σ)

Back to the Bayesics

$p(A|B) = \frac{p(B|A) \cdot p(A)}{p(B)}$

$p(x|\theta) = \frac{p(\theta|x) \cdot p(x)}{\int_a^b p(\theta|x) \cdot p(x) dx}$

Marginal probability a normalization constant

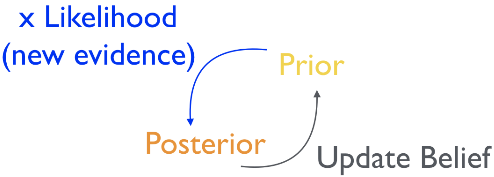
$p(x|\theta) \propto p(\theta|x) \cdot p(x)$

More details? Click Me

Bayes' Theorem — Normal Distributions

$$p(x|\theta) \propto p(\theta|x) \cdot p(x); s.t., \theta = \mu, \sigma$$

$$p(x|\mu, \sigma) \propto \mathcal{L}(\mu, \sigma|x) \cdot p(x)$$

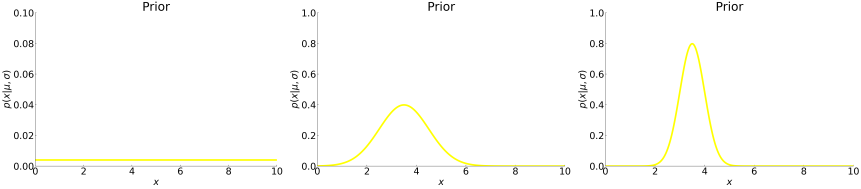


posterior, likelihood, prior can all be defined with a Normal distribution

Prior

No Certainty — Some Certainty — High Certainty

$\mathcal{N}(3.5, \infty^2)$ — $\mathcal{N}(3.5, 1^2)$ — $\mathcal{N}(3.5, 0.5^2)$



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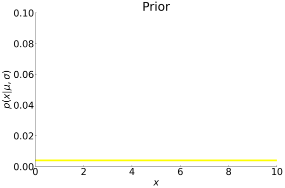
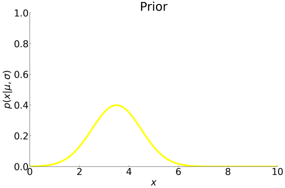
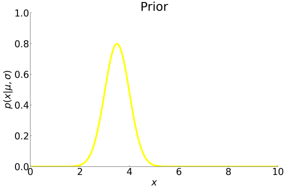
No Certainty — Some Certainty — High Certainty

$$\mathcal{N}(3.5, \infty^2) — \mathcal{N}(3.5, 1^2) — \mathcal{N}(3.5, 0.5^2)$$



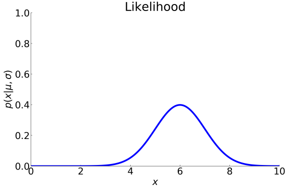




Likelihood

The likelihood of μ, σ given x

$\mathcal{N}(6, 1^2)$



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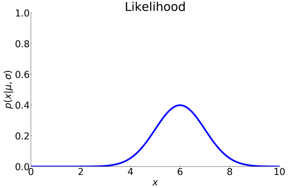

x is the mass of the object that was picked up

(often assumed $\mu = x$ for the likelihood function)

Calculating the Posterior — Analytical

Find a Conjugate Prior

1. IF, the posterior and prior are the same type of distribution, they are conjugate distributions
2. THEN, the prior is a conjugate prior to the likelihood function
3. If we have a conjugate prior we can use hyperparameters to solve the posterior
4. Hyperparameters solved for many distributions: Conjugate Priors - Wikipedia
5. The Normal distribution conjugate prior is the Normal distribution
6. The Bernoulli distribution conjugate prior is the Beta distribution

Hyperparameters

Posterior parameters are a function of the prior and likelihood parameters

Prior $= \mathcal{N}(\mu_0, \sigma_0^2)$; Likelihood $= \mathcal{N}(\mu_1, \sigma_1^2)$; Posterior $= \mathcal{N}(\mu_2, \sigma_2^2)$

$$\mu_2, \sigma_2^2 = \frac{1}{\frac{1}{\sigma_0^2} + \frac{n}{\sigma_1^2}} \cdot \left(\frac{\mu_0}{\sigma_0^2} + \frac{\sum_{i=1}^{n} x_i}{\sigma_1^2} \right), \left(\frac{1}{\sigma_0^2} + \frac{n}{\sigma_1^2} \right)^{-1}$$

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Box-lifting Example:

1. n represents the number of trials
2. x would represent the box weight on the i^{th} trial (e.g., box weight on trial 1: $x_1 = 6$)
3. note: when coding the likelihood function assume $\mu_1 = x_i$

Box-lifting Example — Single Trial

1. Assume you are lifting a box a single trial (n=1)
2. Looking at the box, you originally assumed the box weighs about 3.5N but were uncertain about the estimate ($\sigma_0 = 1$).
3. Once lifted, it feels like the box weighed about 6N ($x_i = \mu_1 = 6$) but you again have some uncertainty on what you felt due to sensory noise ($\sigma_1 = 1$):
4. What is, $p(x|\mu, \sigma)$? That is, what is the probability the box weighs x amount?
5. What is the most likely weight of the box after 1 lift?

Single Trial Example

Prior $= \mathcal{N}(\mu_0, \sigma_0^2)$; Likelihood $= \mathcal{N}(\mu_1, \sigma_1^2)$; Posterior $= \mathcal{N}(\mu_2, \sigma_2^2)$

$$\mu_2, \sigma_2^2 = \frac{1}{\frac{1}{\sigma_0^2} + \frac{n}{\sigma_1^2}} \cdot \left(\frac{\mu_0}{\sigma_0^2} + \frac{\sum_{i=1}^{n} x_i}{\sigma_1^2} \right), \left(\frac{1}{\sigma_0^2} + \frac{n}{\sigma_1^2} \right)^{-1}$$

Single Trial Example

Prior $= \mathcal{N}(\mu_0, \sigma_0^2)$; Likelihood $= \mathcal{N}(\mu_1, \sigma_1^2)$; Posterior $= \mathcal{N}(\mu_2, \sigma_2^2)$

$$\mu_2, \sigma_2^2 = \frac{1}{\frac{1}{\sigma_0^2} + \frac{n}{\sigma_1^2}} \cdot \left(\frac{\mu_0}{\sigma_0^2} + \frac{\Sigma_{i=1}^n x_i}{\sigma_1^2}\right), \left(\frac{1}{\sigma_0^2} + \frac{n}{\sigma_1^2}\right)^{-1}$$

Prior $= \mathcal{N}(3.5, 1^2)$; Likelihood $= \mathcal{N}(6, 1^2)$; n $= 1$

Single Trial Example

Prior $= \mathcal{N}(\mu_0, \sigma_0^2)$; Likelihood $= \mathcal{N}(\mu_1, \sigma_1^2)$; Posterior $= \mathcal{N}(\mu_2, \sigma_2^2)$

$$\mu_2, \sigma_2^2 = \frac{1}{\frac{1}{\sigma_0^2} + \frac{n}{\sigma_1^2}} \cdot \left(\frac{\mu_0}{\sigma_0^2} + \frac{\Sigma_{i=1}^n x_i}{\sigma_1^2}\right), \left(\frac{1}{\sigma_0^2} + \frac{n}{\sigma_1^2}\right)^{-1}$$

Prior $= \mathcal{N}(3.5, 1^2)$; Likelihood $= \mathcal{N}(6, 1^2)$; n $= 1$

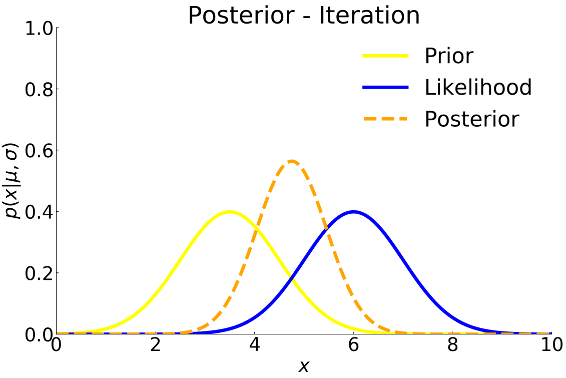
$$4.75, 0.5 = \frac{1}{\frac{1}{1^2} + \frac{1}{1^2}} \cdot \left(\frac{3.5}{1^2} + \frac{6}{1^2}\right), \left(\frac{1}{1^2} + \frac{1}{1^2}\right)^{-1}$$

Posterior $= \mathcal{N}(\mu_2, \sigma_2^2) = \mathcal{N}(4.75, 0.5) = \mathcal{N}(4.75, 0.707^2)$
$\sigma = \sqrt{\sigma^2}$ (e.g.,$0.707 = \sqrt{0.5}$)

Single Trial Example

$$\text{Prior} = \mathcal{N}(3.5, 1^2);\ \text{Likelihood} = \mathcal{N}(6, 1^2)$$

$$\text{Posterior} = \mathcal{N}(4.75, 0.707^2)$$



What is the most likely weight of the box?

Single Trial — Sample Python Code

```
import numpy as np
import math
from pylab import *
from scipy import special

# Calculate Hyperparameters
mu0, sd0 = 3.5, 1.0 # Prior
mu1, sd1 = 6.0, 1.0 # Likelihood
n = 1 # trials
mu2 = (mu0/sd0**2+mu1/sd1**2)/(1/sd0**2+n/sd1**2) #posterior mean
# note below that variance is square rooted (**(1/2.)) to find sd2
sd2 = ((1 / sd0 ** 2 + n / sd1 ** 2)**(-1.0)) ** (1/2.) #posterior stdev

#make and plot Normal curves
dp = 1001 # number of data points
x = np.linspace(0,10,dp) #min, max, number of data points -- defines x axis
pri_0 , like_0 , post_0 = np.zeros(dp), np.zeros(dp), np.zeros(dp)

for i in range(dp):
    pri_0[i]=1/(sd0*(2*math.pi)**(1/2.))*math.exp(-1.0*((x[i]-mu0)**(2.0))/(2*sd0** 2))
    like_0[i]=1/(sd1*(2*math.pi)**(1/2.))*math.exp(-1.0*((x[i]-mu1)**(2.0))/(2*sd1**2))
    post_0[i]=1/(sd2*(2*math.pi)**(1/2.))*math.exp(-1.0*((x[i]-mu2)**(2.0))/(2*sd2**2))

d0 = errorbar(x,pri_0 , linestyle = '-', color = 'yellow')
d1 = errorbar(x,like_0 , linestyle = '-', color = 'blue')
d2 = errorbar(x,post_0 , linestyle = '-', color = 'orange')
show()
```

Box-lifting Example — Multiple Trials

1. Lets assume the same prior, $\mathcal{N}(3.5, 1, 0)$, and likelihood, $\mathcal{N}(6.0, 1.0)$, as the last example.
2. Except, lets say we lift the same box four times ($n = 4$).
3. What is, $p(x|\mu, \sigma)$? That is, what is the probability the box weighs x amount after 4 lifts?
4. What is the most likely weight of the box after 4 lifts?

Hyperparameters — Multiple Trials

Prior $= \mathcal{N}(\mu_0, \sigma_0^2)$; Likelihood $= \mathcal{N}(\mu_1, \sigma_1^2)$; Posterior $= \mathcal{N}(\mu_2, \sigma_2^2)$

$$\mu_2, \sigma_2^2 = \frac{1}{\frac{1}{\sigma_0^2} + \frac{n}{\sigma_1^2}} \cdot \left(\frac{\mu_0}{\sigma_0^2} + \frac{\sum_{i=1}^{n} x_i}{\sigma_1^2} \right), \left(\frac{1}{\sigma_0^2} + \frac{n}{\sigma_1^2} \right)^{-1}$$

Hyperparameters — Multiple Trials

Prior $= \mathcal{N}(\mu_0, \sigma_0^2)$; Likelihood $= \mathcal{N}(\mu_1, \sigma_1^2)$; Posterior $= \mathcal{N}(\mu_2, \sigma_2^2)$

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Prior $= \mathcal{N}(3.5, 1^2)$; Likelihood $= \mathcal{N}(6, 1^2)$; $n = 4$

Hyperparameters — Multiple Trials

Prior $= \mathcal{N}(\mu_0, \sigma_0^2)$; Likelihood $= \mathcal{N}(\mu_1, \sigma_1^2)$; Posterior $= \mathcal{N}(\mu_2, \sigma_2^2)$

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Prior $= \mathcal{N}(3.5, 1^2)$; Likelihood $= \mathcal{N}(6, 1^2)$; $n = 4$

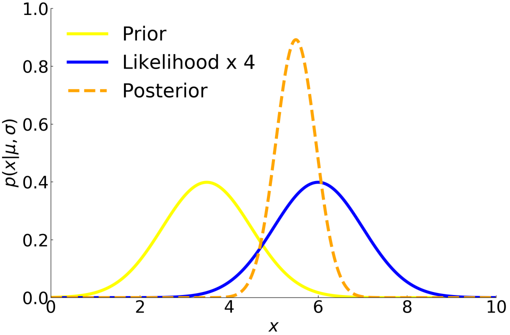
$$5.5, 0.2 = \frac{1}{\frac{1}{1^2} + \frac{4}{1^2}} \cdot \left(\frac{3.5}{1^2} + \frac{6+6+6+6}{1^2} \right), \left(\frac{1}{1^2} + \frac{4}{1^2} \right)^{-1}$$

Posterior $= \mathcal{N}(\mu_2, \sigma_2^2) = \mathcal{N}(5.5, 0.2) = \mathcal{N}(5.5, 0.447^2)$

Hyperparameters — Multiple Trials

Prior $= \mathcal{N}(3.5, 1^2)$; Likelihood $= \mathcal{N}(6, 1^2)$, $n = 4$

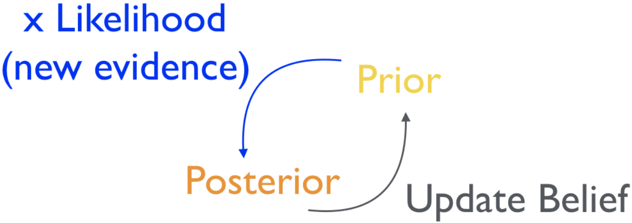
Posterior $= \mathcal{N}(5.5, 0.447^2)$



What is the most likely weight of the box after 4 lifts?

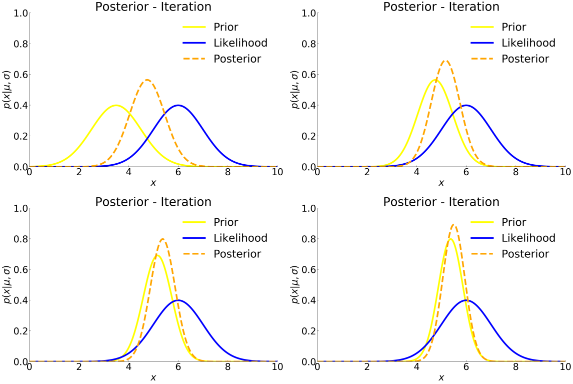
Multiple Trials — Alternative

1. Use the Single Trial equation and repeat it four times
2. Posterior becomes the Prior on the next iteration



Multiple Trials — Alternative

1. Use the Single Trial equation and repeat it four times
2. Posterior becomes the Prior on the next iteration

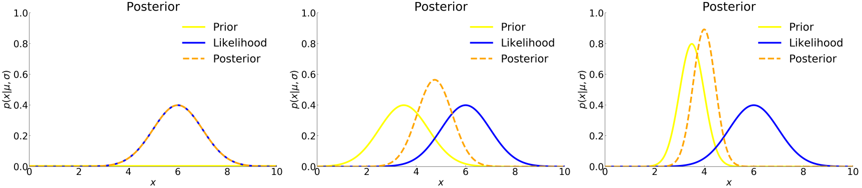


Bayes' Theorem can capture ADAPTATION

Prior Influence

No Certainty — Some Certainty — High Certainty

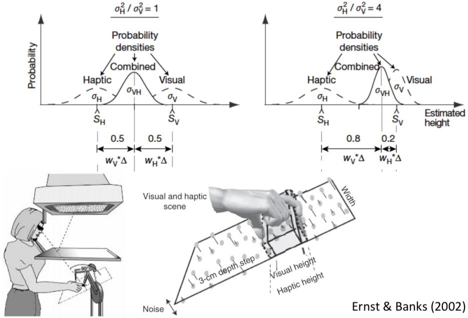
$\mathcal{N}(3.5, \infty^2)$ — $\mathcal{N}(3.5, 1^2)$ — $\mathcal{N}(3.5, 0.5^2)$



Bayes' Theorem can capture PRIOR beliefs

Multiple Senses

Bayesian Integration



Ernst & Banks (2002) Nature

Multiple Senses

Bayes' Theorem can account for MULTIPLE SENSES

(e.g., McGurk Effect)

Table 3.1

Distribution	**Argument**	**Mean**	**Variance**
Auditory noise distribution	auditory measurement, x_A	auditory stimulus s_A	σ_A^2
visual noise distribution	visual measurement, x_V	visual stimulus s_V	σ_V^2
prior distribution	hypothesized stimulus s	μ	σ_p^2
auditory likelihood function	hypothesized stimulus s	measurement, x_A	σ_A^2
visual likelihood function	hypothesized stimulus s	measurement, x_V	σ_V^2
combined likelihood	hypothesized stimulus s	$\dfrac{\frac{x_A}{\sigma_A^2}+\frac{x_V}{\sigma_V^2}}{\frac{1}{\sigma_A^2}+\frac{1}{\sigma_V^2}}$	$\left(\frac{1}{\sigma_A^2}+\frac{1}{\sigma_V^2}\right)^{-1}$
posterior distribution	hypothesized stimulus s	$\dfrac{\frac{x_A}{\sigma_A^2}+\frac{x_V}{\sigma_V^2}+\frac{\mu}{\sigma_p^2}}{\frac{1}{\sigma_A^2}+\frac{1}{\sigma_V^2}+\frac{1}{\sigma_p^2}}$	$\left(\frac{1}{\sigma_A^2}+\frac{1}{\sigma_V^2}+\frac{1}{\sigma_p^2}\right)^{-1}$

Hyperparameters for 2 Likelihood terms (vision and auditory).

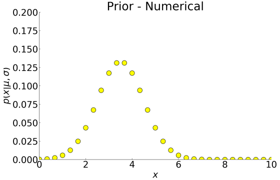
Equations here for single trial only.

Describing the Posterior — Cost functions

1. mode = maximum likelihood estimate
2. mean = minimize sum of squared error (think of linear regression)
3. median = minimize sum of absolute error (robust to outliers)
4. Nervous system: Cashaback et al., 2017 and Kording et al., 2004
   - depends on the type of feedback
   - the size of the errors

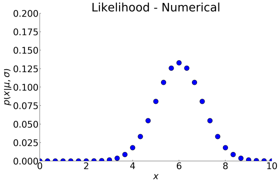
Numerical

Numerical — Estimating the Posterior



X

Point-Wise Multiplication



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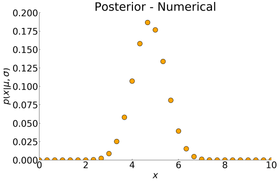
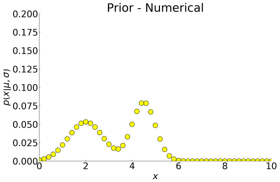


Numerical — Sample Python Code

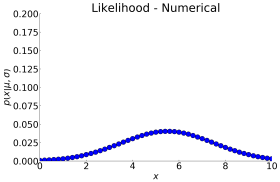
```
import numpy as np
import math
from pylab import *

iterations = 4
dp = 101 # number of data points
x = np.linspace(0,10,dp) #min, max, number of data points

mu0, sd0 = 3.5, 1.0 # prior
mu1, sd1 = 6.0, 1.0 # likelihood
prior_0, like_0, posterior_0 = np.zeros(dp), np.zeros(dp), np.zeros(dp)
for i in range(dp):
    prior_0[i]=1/(sd0*(2*math.pi)**(1/2.))*math.exp(-1.0*((x[i]-mu0)**(2.0))/(2*sd0**2))
    like_0[i]=1/(sd1*(2*math.pi)**(1/2.))*math.exp(-1.0*((x[i]-mu1)**(2.0))/(2*sd1**2))

#normalize each distribution to 1.0
prior_0 = prior_0 / np.sum(prior_0)
like_0 = like_0 / np.sum(like_0)

# iterate
for i1 in range(iterations):
    #normalized the posterior to 1.0 on each iteration
    posterior_0 = (like_0 * prior_0) / np.sum(like_0 * prior_0)
    plot(x,posterior_0)
    show()
    prior_0 = posterior_0
```

Numerical — Curvy Posteriors

X



Any Shape



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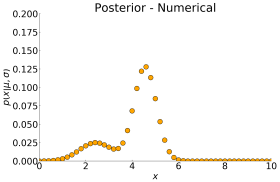

Numerical — Comments

1. Normalize the posterior (sum to 1.0)
2. Examples also normalized the likelihood and prior
   - Likelihood may not necessarily sum to 1.0 in many instances (OK with Normal)
3. Fine vs. Course Grid
   - tradeoff between accuracy and efficiency

Summary

Bayes' Theorem

1. Point Probabilities
2. Continuous Probabilities
   - Analytical
   - Numerical
3. Prior Beliefs
4. Adaptation
5. Multisensory Integration

Questions???

Homework

See Handout

Next Class

MODULE 2 — OUTPUTS

1. Muscle Function
   a. Alpha motor neuron
   b. Neuromuscular junction, sarcoplasmic reticulum
   c. cross-bridges
   d. force-length curve (active and passive)
   e. force-velocity curve
   f. tendon compliance

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