## Part II Overview

- Information and decision making, Chs. 13-14
- Signal coding, Ch. 15
- Signal economics, Chs. 16-17
- Optimizing communication, Ch. 19
- Signal honesty, Ch. 20


## Information and Decisions

- Signals and coding
- Information: value versus amount
- Information in a signal set
- Bayesian updating
- Discrete decision rules
- Signal detection theory
- Reading for Lecture 12
- Ch 13 pp 388 to 395, 402-406, box 1
- Ch 14 pp 419 to 438
- Ch 15 pp 455-460


## Signal definitions



Figure 12.3 Summary of terms used to classify animal signals. Context refers to the general situation in which the signal exchange occurs. Two contexts, conflict resolution and territorial defense are listed here. Within each context, a variety of questions may be asked by receivers. For each, there are alternative conditions (answers) that may be true. Senders have access to several alternative signals that they associate with these alternative conditions according to the signal code. Those signals assigned to a particular question constitute a signal set; the entire list of signals for a species is its signal repertoire.

## Assumptions

- Senders produce signals in order to provide honest (accurate) information to receivers
- Dishonest signaling will be considered later
- Communication involves signal production, transmission, and reception. All three processes influence the accuracy of any coding scheme


## Coding matrix



Probability of giving a signal in each condition. Sender matrix must be similar to Receiver matrix for communication to occur.

| Coding | Coding summary <br> rule |
| :--- | :--- |
| $\left\{P\left(S_{j} \mid C_{i}\right)\right\}$ |  |


| No coding |  | $\mathrm{C}_{1}$ | $\mathrm{C}_{2}$ | $\mathrm{C}_{3}$ |
| :---: | :---: | :---: | :---: | :---: |
|  | $S_{1}$ | 0.33 | 0.33 | 0.33 |
|  | $S_{2}$ | 0.33 | 0.33 | 0.33 |
|  | $S_{3}$ | 0.33 | 0.33 | 0.33 |

Perfect
coding

|  | $C_{1}$ | $C_{2}$ | $C_{3}$ |
| :---: | :---: | :---: | :---: |
|  | 1.0 | 0 | 0 |
| $S_{2}$ | 0 | 1.0 | 0 |
| $S_{3}$ | 0 | 0 | 1.0 |
|  |  |  |  |

Specific but not unique coding
Unique but not specific coding

|  | $C_{1}$ | $C_{2}$ | $C_{3}$ |
| :---: | :---: | :---: | :---: |
|  | 1.0 | 1.0 | 0 |
| $S_{2}$ | 0 | 0 | 1.0 |
| $S_{3}$ | 0 | 0 | 0 |
|  |  |  |  |


|  | $C_{1}$ | $C_{2}$ | $C_{3}$ |
| :---: | :---: | :---: | :---: |
| $S_{1}$ | 0.5 | 0 | 0 |
| $S_{2}$ | 0 | 1.0 | 0 |
| $S_{3}$ | 0 | 0 | 1.0 |
| $S_{4}$ | 0.5 | 0 | 0 |

Neither unique nor specific coding

- No coding - all probabilities equal
- Perfect - each signal occurs with only 1 condition
- Specific - 1 signal per condition, but multiple conditions per signal
- Unique - one or more signals per condition, no overlap of signals


## Value versus amount of information

- The average value of information is the difference in payoff with a signal versus without a signal
- Value and amount are related, but not the same
- Increasing the amount of information generally
- increases probability of a correct decision by receiver
- increases costs of signal for senders and receivers
- Consequently, intermediate levels of information tend to maximize value of information and are optimal


## Problem: How can we

 measure the amount of information needed for any question?Estrous female? Cuckoo egg?


Aggressive level?

Answer: Use \# of binary questions

$$
\mathrm{H}=\log _{2} \mathrm{M}
$$

where M is the possible number of equally likely answers


## Measuring information in a signal

- Assume a female has a pre-existing estimate of the probability that a male is a conspecific, $\mathrm{P}_{0}$ ( $a$ priori probability)
- After receiving a signal from him, she changes her estimate to $\mathrm{P}_{1}$ (a posteriori probability).
- How much information has she acquired?

$$
\begin{aligned}
& \mathrm{H}_{\mathrm{T}}=\log _{2}\left(\mathrm{P}_{1} / \mathrm{P}_{0}\right) \text { bits of information } \\
& \left(\mathrm{H}_{\mathrm{T}}=\text { information transferred }\right)
\end{aligned}
$$

## Information when coding is perfect

- Assume that code between signal and condition is perfect
- Song identifies male species with no error
- Fast song conspecific, slow song heterospecific
- Then, once a female hears a male sing, she knows his species, i.e. $P_{1}=1$
- In this case

$$
\begin{aligned}
& \mathrm{H}_{\mathrm{T}}(\text { fast song })=\log _{2}\left(1 / \mathrm{P}_{0}\right)= \\
& \log _{2}(1)-\log _{2}\left(\mathrm{P}_{0}\right)=-\log _{2}\left(\mathrm{P}_{0}\right)
\end{aligned}
$$

- If M alternative signals are equally likely, then the a priori probability will be $1 / \mathrm{M}$ and
$-\mathrm{H}_{\mathrm{T}}=-\log _{2}\left(\mathrm{P}_{0}\right)=-\log _{2}(1 / \mathrm{M})=\log _{2}(\mathrm{M})$


## Average information

Figure 13.2 Average information as a function of a priori probabilities for a signal set with two alternative conditions and perfect coding. The horizontal axis shows the probability that one of two alternative signals will be received; the vertical axis shows the average amount of information, in bits.


Maximum information occurs when $\mathrm{P}_{\mathrm{o}}=1 / \mathrm{M}$

## Information in a signal set

- If the a priori probability that a signal I will be given is $\mathrm{P}_{\mathrm{i}}$ and
- the information provided when I is received is $\mathrm{H}_{\mathrm{i}}$ bits, then
- the average information transferred when several signals are possible is

$$
\mathrm{H}_{\mathrm{T}}=\Sigma \mathrm{P}_{\mathrm{i}} \mathrm{H}_{\mathrm{i}}
$$

- when coding is perfect, $\mathrm{H}_{\mathrm{i}}=-\log _{2}\left(\mathrm{P}_{\mathrm{i}}\right)$, so

$$
\mathrm{H}_{\mathrm{T}}=-\Sigma \mathrm{P}_{\mathrm{i}} \log _{2}\left(\mathrm{P}_{\mathrm{i}}\right) \quad \text { (Shannon-Weiner) }
$$

## Prob. of fish attack by display (independent signals)

|  | Fins <br> Raised | Fins <br> Lowered | Sum |
| :---: | :---: | :---: | :---: |
| Dark | 0.48 | 0.32 | 0.80 |
| Light | 0.12 | 0.08 | 0.20 |
| Sum | 0.6 | 0.4 | 1.00 |

Because signals are independent, information content of display $=$ $\mathrm{H}_{\mathrm{T}}($ Display $)=\mathrm{H}_{\mathrm{T}}($ Color $)+\mathrm{H}_{\mathrm{T}}($ Fins $)=$
$-\left(0.8 \log _{2}(0.8)+0.2 \log _{2}(0.2)\right)+\left(0.6 \log _{2}(0.6)+0.4 \log _{2}(0.4)\right)$
$=1.69$ bits

## Prob. of fish attack by display (non-independent signals)

|  | Raised | Lowered | Sum |
| :---: | :---: | :---: | :---: |
| Dark | 0.56 | 0.24 | 0.80 |
| Light | 0.04 | 0.16 | 0.20 |
| Sum | 0.6 | 0.4 | 1.00 |

Signals are not independent, information content of display $=$ $\mathrm{H}_{\mathrm{T}}($ Display $)=-\sum \sum \mathrm{P}\left(\mathrm{A}_{\mathrm{i}}\right.$ and $\left.\mathrm{B}_{\mathrm{j}}\right) \log _{2} \mathrm{P}\left(\mathrm{A}_{\mathrm{i}}\right.$ and $\left.\mathrm{B}_{\mathrm{j}}\right)=$
$-\left(0.56 \log _{2}(0.56)+0.24 \log _{2}(0.24)+\left(0.04 \log _{2}(0.04)+0.16 \log _{2}(0.16)\right)\right.$
$=1.57$ bits

## Sources of error in signal transmission

- Sender
- Imperfect coding by sender
- Error in production
- Propagation
- Distortion by environment
- Masking by noise
- Receiver
- Error in discriminating signals from alternatives
- Error in associating signals with conditions (imperfect receiver coding)


## Conditional probabilities

- If there is some error in associating signals with a condition, four possible combinations of signals and conditions:
- $\left(\mathrm{C}_{1}\right.$ and $\left.\mathrm{S}_{1}\right),\left(\mathrm{C}_{2}\right.$ and $\left.\mathrm{S}_{2}\right)$ are accurate signals
- $\left(\mathrm{C}_{1}\right.$ and $\left.\mathrm{S}_{2}\right),\left(\mathrm{C}_{2}\right.$ and $\left.\mathrm{S}_{1}\right)$ are error signals
- These can be expressed as conditional probabilities:
$-\mathrm{P}\left(\mathrm{C}_{1} \mid \mathrm{S}_{1}\right)$ is the probability of condition 1 given the observation of signal 1
- Also $\mathrm{P}\left(\mathrm{C}_{2} \mid \mathrm{S}_{2}\right), \mathrm{P}\left(\mathrm{C}_{1} \mid \mathrm{S}_{2}\right)$ and $\mathrm{P}\left(\mathrm{C}_{2} \mid \mathrm{S}_{1}\right)$


## Signals with error



Conditional probabilities for each signal sum to 1 How should the receiver interpret the signal?

## Optimal updating: Bayes theorem

- If the receiver knows
- relative probability of different conditions $\mathrm{P}\left(\mathrm{C}_{1}\right)$ and $\mathrm{P}\left(\mathrm{C}_{2}\right)$
- and average chances of correct and incorrect transmission $\mathrm{P}\left(\mathrm{S}_{1} \mid \mathrm{C}_{1}\right) \mathrm{P}\left(\mathrm{S}_{1} \mid \mathrm{C}_{2}\right), \mathrm{P}\left(\mathrm{S}_{2} \mid \mathrm{C}_{2}\right)$ and $\mathrm{P}\left(\mathrm{S}_{2} \mid \mathrm{C}_{1}\right)$
- What is the probability that $\mathrm{C}_{1}$ is true if $\mathrm{S}_{1}$ is observed?
- Then optimal updating is

$$
\mathrm{P}\left(\mathrm{C}_{1} \mid \mathrm{S}_{1}\right)=\mathrm{P}\left(\mathrm{C}_{1}\right) \mathrm{P}\left(\mathrm{~S}_{1} \mid \mathrm{C}_{1}\right) /\left[\mathrm{P}\left(\mathrm{C}_{1}\right) \mathrm{P}\left(\mathrm{~S}_{1} \mid \mathrm{C}_{1}\right)+\mathrm{P}\left(\mathrm{C}_{2}\right) \mathrm{P}\left(\mathrm{~S}_{1} \mid \mathrm{C}_{2}\right)\right]
$$

$=$ prob condition $1 *$ prob signal 1 if condition $1 /$ prop. time observe signal 1

## Bayesian updating problem

- Female frog assessing male song
- Conspecifics sing fast $70 \%$, slow $30 \%$
- Heterospecifics sing fast $40 \%$, slow $60 \%$
- Population is 50:50 two species
- If female hears a fast song, what is likelihood of a conspecific?
$\mathrm{P}($ Con $\mid$ Fast $)=\mathrm{P}($ Cons $) \mathrm{P}($ Fast 1 Cons $) /[\mathrm{P}($ Cons $) \mathrm{P}($ FastlCons $)+\mathrm{P}($ Hetero $) \mathrm{P}($ Fast|Hetero $)]$
$\mathrm{P}($ ConlFast $)=(0.5)(0.7) /[(0.5)(0.7)+(0.5)(0.4)]=0.636$
- What is likelihood of conspecific if she hears a slow song?
$\mathrm{P}($ ConlSlow $)=\mathrm{P}($ Cons $) \mathrm{P}($ Slow 1 Cons $) /[\mathrm{P}($ Cons $) \mathrm{P}($ SlowlCons $)+\mathrm{P}($ Hetero $) \mathrm{P}($ Slow 1 Hetero $)]$
$\mathrm{P}($ ConlSlow $)=(0.5)(0.3) /[(0.5)(0.3)+(0.5)(0.6)]=0.333$
- Note that information change need not be symmetrical
- rarer song provides more information


## Sequential Bayesian updating

- In sequential assessment, the a posteriori probability from the previous signal becomes the a priori probability for the next
- Female heard one fast song, updated her assessment of male species
- Conspecifics $=63.6 \%$, heterospecific $=33.3 \%$
- If female hears another fast song, what is likelihood of a conspecific?

$$
\begin{gathered}
\mathrm{P}(\text { Con } \mid \text { Fast })=\mathrm{P}(\text { Cons }) \mathrm{P}(\text { Fast|Cons }) /[\mathrm{P}(\text { Cons }) \mathrm{P}(\text { Fast|Cons })+\mathrm{P}(\text { Hetero }) \mathrm{P}(\text { Fast|Hetero })] \\
\mathrm{P}(\text { Con } \mid \text { Fast })=(0.636)(0.7) /[(0.6 .36)(0.7)+(0.364)(0.4)]=0.754
\end{gathered}
$$

- Female's estimate of singing male as a conspecific has risen to $75.4 \%$ after two fast songs


## Sequential Bayesian updating



- A series of FFSF gives same final probability as a series of SFFF or FSFF or FFFS
- FFSS $\neq 50 \%$ Why?
- $\operatorname{FFFF} \neq 1$ Why?


## Sequential Bayesian updating



## Average information with sequential sampling



Sequential updating provides progressively less information with repeated sampling.

## Do animals use Bayesian updating?

- Requires knowledge of
-Probabilities of conditions
-Probabilities of correct and incorrect transmission
-Gives ideal that animals can achieve
- Alternative: animals may use simple rules of thumb
- Best-of-N samples
- Fixed sampling time
- Linear operators


## Decision rules with perfect information

- After a signal, the receiver has an updated estimate (posterior probability) that Condition 1 is true.
- The optimal action by a receiver is to establish a critical probability $\left(\mathrm{P}_{\mathrm{c}}\right)$ for a given response
- If posterior prob above the critical threshold do Act ${ }_{1}$
- If below the critical threshold do $\mathrm{Act}_{2}$
- $P_{c}$ depends on the receiver's payoff matrix, i.e. the costs and benefits associated with either correct actions or mistakes


## Payoff matrices

- Consider a female bird trying to choose a healthy male

- Determine the critical probability for favoring acceptance over rejection as

$$
\mathrm{P}_{\mathrm{c}}=\left(\mathrm{R}_{22}-\mathrm{R}_{12}\right) /\left[\left(\mathrm{R}_{22}-\mathrm{R}_{12}\right)+\left(\mathrm{R}_{11}-\mathrm{R}_{21}\right)\right]
$$

## Decisions with imperfect information

- $\mathrm{Q}=$ correlation between the signal and the condition
- equivalent to the conditional probability $\mathrm{P}(\mathrm{SIC})$
- There is a critical value of $\mathrm{Q}\left(\mathrm{Q}_{\mathrm{c}}\right)$ that must be obtained before a receiver should attend to a signal.
- increases with increasing $\mathrm{P}_{\mathrm{c}}$ (critical probability)
- decreases with increasing $\mathrm{P}_{1}$ (prior probability)


## Decisions with imperfect information



## Coding options

Continuous $\underbrace{\substack{\text { Discrete/continuous }}}_{\text {Condition }}$\begin{tabular}{l}
Discrete <br>
(small $N$ )

$\quad$

Discrete <br>
(large $N$ )
\end{tabular}

## Signal detection theory



- Decreasing $w_{c}$ decreases $P_{\text {miss }}$, but increases $P_{\text {false alarm }}$
- Increasing $\mathrm{w}_{\mathrm{c}}$ increases $\mathrm{P}_{\text {correct reject }}$, but decreases $\mathrm{P}_{\text {hit }}$


## Signal detection theory



ROC $=$ receiver operating characteristic: plots correct detection against false alarms. As the threshold criterion moves left to right, the $\mathrm{P}_{\mathrm{CD}}$ vs $\mathrm{P}_{\mathrm{FA}}$ moves down to the left.
$d^{\prime}=$ receiver sensitivity (z score)
Greater separation between signal and noise increases d’.
(A)


(B)


(C)



## ROC plots and d'

- As d’ increases, receiver becomes more accurate in discrimination
- Receiver operating characteristic (ROC) plots illustrate change in tradeoff of errors


## Optimal sensitivity



- Intermediate sensitivity is usually optimal because there are costs associated with evolving increased sensitivity
- Cost function $\left(K\left(d^{\prime}\right)\right)$ for receiver sensitivity may increase faster than linear

