

The 'Bayesian Brain'

Readings: Knill & Pouget, *TINS*, 2004

Uncertainty everywhere

- Humans and other animals operate in a world of sensory **uncertainty**:
 - e.g. mapping of 3D objects to 2D image
 - intrinsic limitations of the sensory systems (e.g. number and quality of receptors in the retina)
 - neural noise
- > **multiple interpretations** about the world are possible;
- The brain must deal with this uncertainty to generate perceptual representations and guide actions.
- Perception as **unconscious, probabilistic inference**

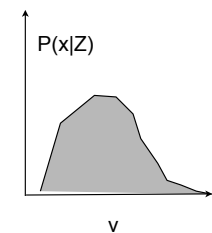
Example: Multi-sensory integration

- How to integrate information coming from different senses?
- example: ventriloquism.
 - **sound** has uncertain origin.
 - **visual** image is that the puppet is talking.
- at **which stage** are the informations integrated to provide estimate of spatial origin of the sound ? **how?**



Bayesian coding hypothesis (1)

- Hypothesis: information provided by sensory systems has the form of a **conditional probability density function**
- e.g. the position of an object is not a single number, x , but $P(x|Z)$, where Z is the available data
- = stores likelihoods = '**generative models**', or '**forward model**' of the world, $P(Z|x)$, and **prior** knowledge / state of the world, $P(x)$.
- Given new data Z , the brain computes $P(x|Z)$



$$P(x|Z) = \frac{P(x, Z)}{P(Z)} = \frac{P(Z|x)P(x)}{P(Z)}$$

Bayes theorem

Bayesian coding hypothesis (2)

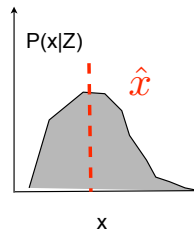
- Benefits:

- **integrate** information efficiently over **space & time**
- integrate information efficiently from **different sensory cues and modalities**
- **propagate** information without committing too early to particular interpretations.

- **Commit as late as possible**, then collapsing the probability distribution into a single number = decision, or action taken.

- How to do that depends on cost function :

$$\hat{x} = \operatorname{argmax}_x P(x|Z) \quad \text{max of the posterior}$$



Estimators and cost functions

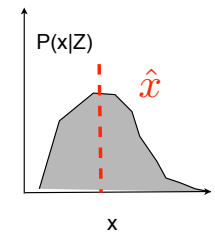
- How to do that depends on cost function :

- one option is to take the **max of the posterior**

$$\hat{x} = \operatorname{argmax}_x P(x|Z)$$

this is known to optimize a cost function that is 0

when $\hat{x} = x$ and $e = \text{cst}$ otherwise.



max of the posterior

- another option is to take the **mean of the posterior**

$$\hat{s} = \int xp(x|Z)dx$$

which minimizes the mean squared error $(\hat{x} - x)^2$

Are Humans Bayes - optimal?

- Humans not optimal / achieving the level of performance afforded by the uncertainty in the physical stimulus (e.g. movies)

- The question is:

Do the neural computations take into account the uncertainty at each stage of processing?

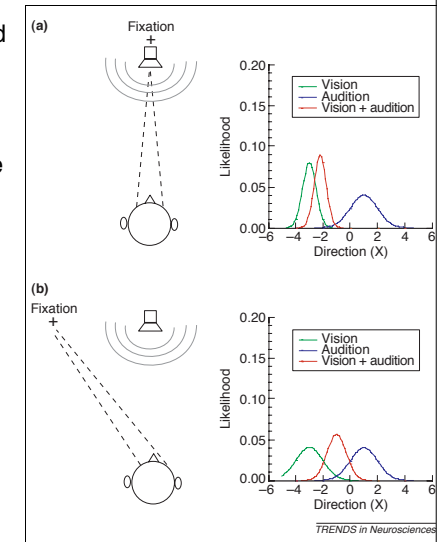
- Bayesian hypothesis makes a lot of **testable predictions** on how different sources of uncertainty should be integrated. Valid?

Cue Integration (1) : qualitative predictions

- e.g. **integration** between visual and auditory information

- **prediction 1 (position)**: if visual cue is more reliable, then final estimate is shifted towards visual cue.

- **prediction 2 (variance or discrimination threshold)**: Final discrimination threshold lower than that for each modality ; varies if reliability of one modality varies.



Cue Integration (2): Theory

- Theory tells us how **posterior** depends on individual likelihoods:

$$\hat{x} = \operatorname{argmax}_x P(x|d_1, d_2)$$

$$P(x|d_1, d_2) = \frac{P(d_1, d_2|x)P(x)}{P(d_1, d_2)} \propto P(d_1|x)P(d_2|x)P(x)$$

- Assuming that the **likelihood are gaussian**, i.e.

$$P(d_1|x) \propto \exp\left(-\frac{(d_1 - x)^2}{2\sigma_1^2}\right)$$

- We can determine **mean** and **width of posterior** (gaussian):

$$P(d_1|x)P(d_2|x) \propto \exp\left(-\frac{(d_1 - x)^2}{2\sigma_1^2} - \frac{(d_2 - x)^2}{2\sigma_2^2}\right) \propto \exp\left[-\frac{x - \frac{\sigma_2^2 d_1 + \sigma_1^2 d_2}{\sigma_1^2 + \sigma_2^2}}{2\sigma_1^2 \sigma_2^2 / (\sigma_1^2 + \sigma_2^2)}\right]^2$$

Cue Integration (3): Theory

- If we know mean estimate and variance for each modality in isolation, we can deduce **mean of bimodal estimate**:

$$\mu = \frac{\sigma_2^2}{\sigma_1^2 + \sigma_2^2} d_1 + \frac{\sigma_1^2}{\sigma_1^2 + \sigma_2^2} d_2$$

pushed towards more reliable cue

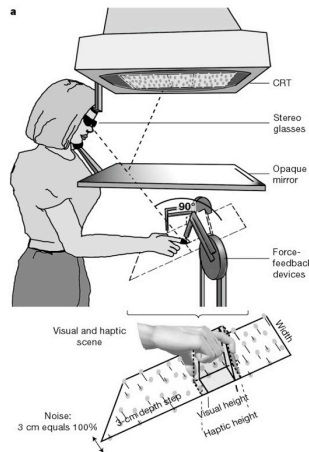
- and **discrimination threshold**

$$T_{1,2}^2 \propto \sigma_{1,2}^2 = \sigma_1^2 \sigma_2^2 / (\sigma_1^2 + \sigma_2^2)$$

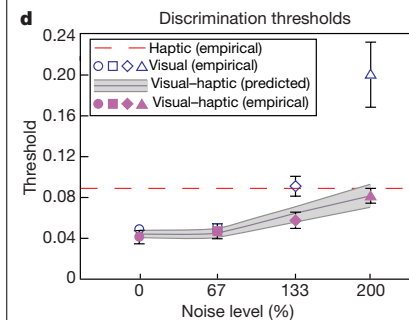
smaller than 1 or 2 alone

Cue Integration (4): Ernst and Banks, *Nature*, 2002

- visual + haptic cues**
- vary **noise level / visual cue**
- compute **discrimination threshold** for each cue alone, or when both are present.



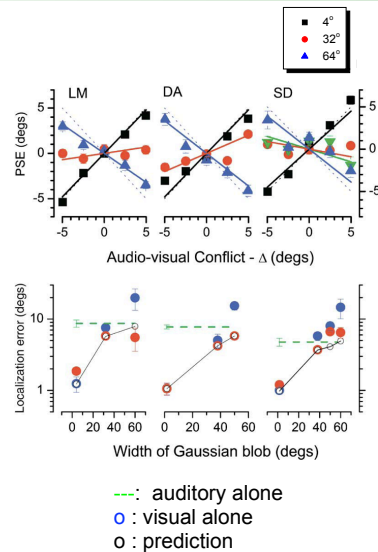
Cue Integration (5): Ernst and Banks, *Nature*, 2002



- height judgment follows **optimal integration** of visual and haptic cues.
- '**visual capture**' for low visual noise
- '**haptic capture**' for high visual noise
- instantaneous '**switch**'
- numerous studies replicate this result in a variety of paradigms.

Cue Integration (6): Ventriloquist effect

- Alais & Burr, *Curr Biol*, 2004
- **visual** blob of various size + **auditive** 'click', possibly in conflict.
- measure both estimate of position (**mean**), and **discrimination** threshold
- near optimal integration
- visual capture for small blobs
- auditive capture for large blobs

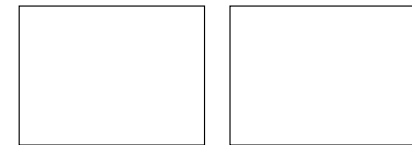
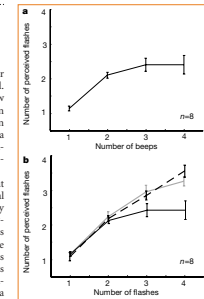


Cue Integration (7)

- capture of vision by sound
- Shams et al, *Nature*, 2000.

What you see is what you hear

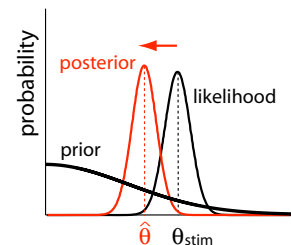
Illusions
Vision is believed to dominate our multisensory perception of the world. Here we overturn this established view by showing that auditory information can qualitatively alter the perception of an unambiguous visual stimulus to create a striking visual illusion. Our findings indicate that visual perception can be manipulated by other sensory modalities. We have discovered a visual illusion that is induced by sound: when a single visual flash is accompanied by multiple auditory beeps, the single flash is incorrectly perceived as multiple flashes. These results were obtained by flashing a uniform white disk (subtending 2 degrees at 5 degrees eccentricity) for a variable number of times (50 milliseconds apart) on a black background. Flashes were accompanied by a



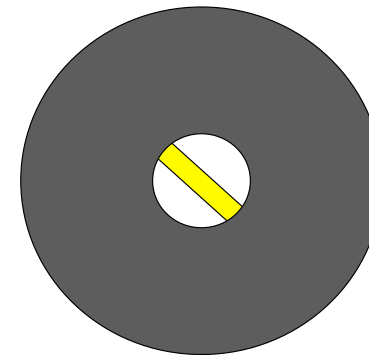
<http://shamslab.psych.ucla.edu/demos/>

Other predictions of Bayesian theory

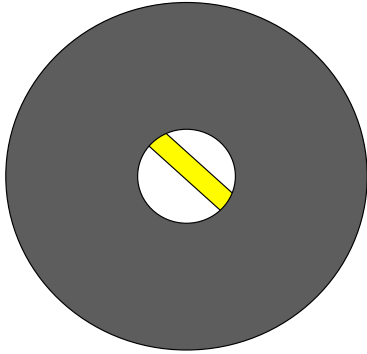
- **Prior knowledge** about the world can be used to interpret data in situation of uncertainty.
- Prediction: **the more uncertain the data, the more the prior should influence the interpretation.**
- The priors should reflect the **statistics of the sensory world.**



Interpreting motion (1): the aperture problem

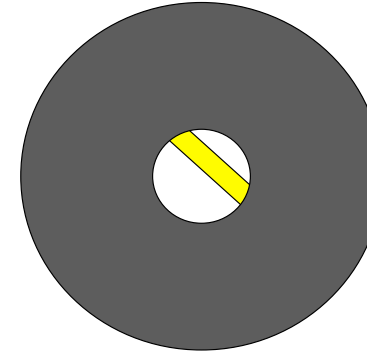


Interpreting motion (1): the aperture problem

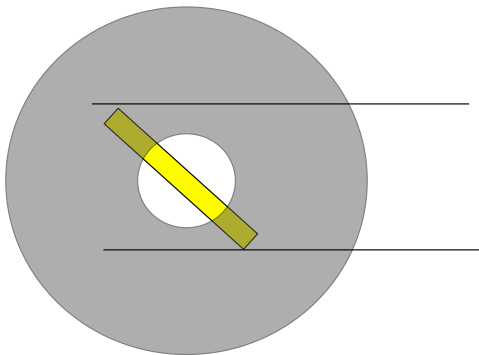


Interpreting motion (1): the aperture problem

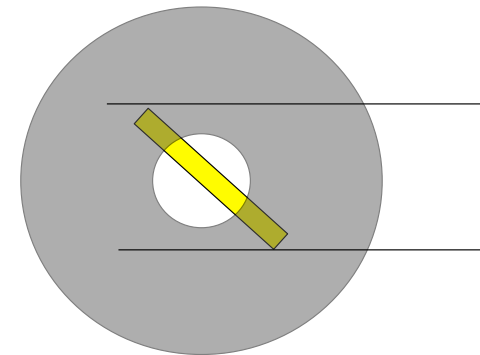
- what is the direction of the line?



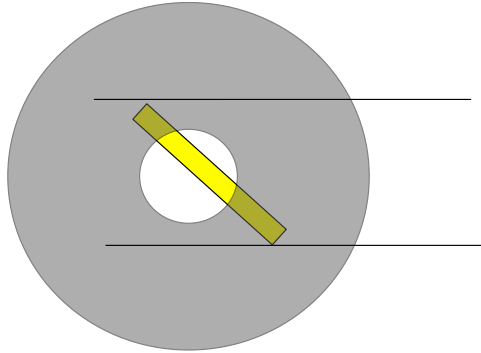
Interpreting motion (1): the aperture problem



Interpreting motion (1): the aperture problem

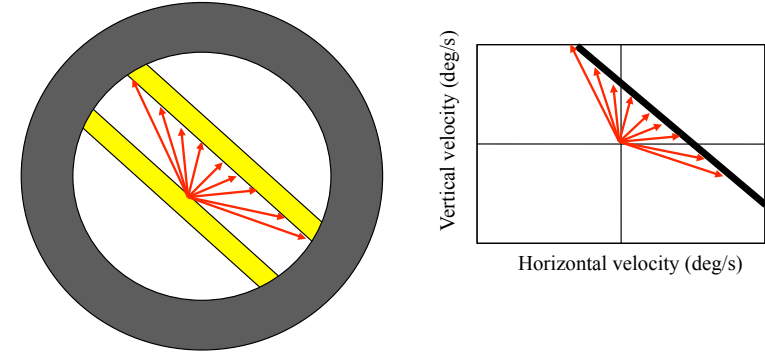


Interpreting motion (1): the aperture problem



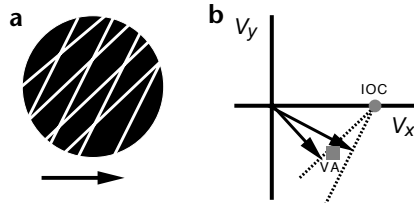
Interpreting motion (2): the aperture problem

- Motion shown in an aperture is fundamentally ambiguous; it can be interpreted in an infinite number of ways
- which one is chosen? why?



Interpreting motion (3): the aperture problem

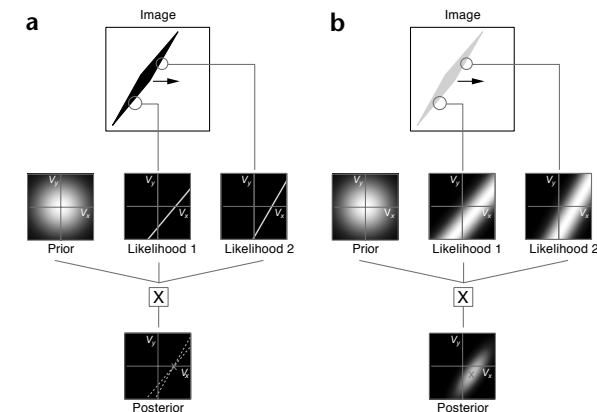
- **More complex stimuli** can be constructed, by adding more segments of ambiguous motions, e.g. plaid, or rhombus.
- How is the system going to integrate the different possible interpretations?
- classical models: intersection of constraints (**IOC**), Vector Averaging (**VA**), feature tracking.
- do not capture the complexity of available data.



<http://www.cs.huji.ac.il/~yweiss/Rhombus/rhombus.html>

Interpreting motion : A Prior on Low Speeds (1)

- Hypothesis: humans tend to **favor slower motions**
- Use a (gaussian) **prior on low speeds** (centered at 0).



Weiss, Adelson & Simoncelli, *Nat Neuro*, 2002

interpreting motion : A Prior on Low Speeds (2)

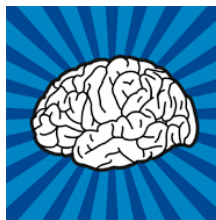
- provides a very **simple model** which explains a **large variety of psychophysical effects** / perception of plaids, rhombus and plaids, barber pole and effects of contrast [Weiss et al, 2004]
- **Thomson effect**: humans tend to underestimate speed at low contrast (why drivers tend to speed up in the fog)
- Stocker & Simoncelli (2005) measure the shape of the prior.
- **illusions as 'optimal percepts'**.

interpreting motion : A Prior on direction of lightning



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- elegant psychophysics looking for neural basis.



Neural implementation ?

- How do populations of neurons represent **uncertainty** ?
- Does neural activity represent **probabilities**? (log probabilities?)
- Can we distinguish stages where the **likelihoods**, **priors**, **posterior** could be 'measured' experimentally ?
- Can networks of neurons **implement optimal inference**?
- How can we discover the **priors** used by the brain?
- How can a prior be **implemented**? (baseline - spontaneous activity, number of neurons, gain, connectivity?).
- Recently, active topic of theoretical research (A. Pouget, S. Deneve, P. Dayan, R. Rao).
- promising direction for PhD project :-)



Thanks !

This is the end of CCN lectures

brain science:
open the black box

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