

# How Key Structures in the Brain Combine Sensory Modalities

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# Overview

- Examples of multisensory processing
  - McGurk-MacDonald Effect
  - Rubber Hand Effect
  - Extent and neural basis
- An example of multisensory processing
  - Superior colliculus
  - Topographic maps
  - Sensory alignment, integration and cortical feedback
- Computational principles
  - Sensory alignment through association



# Suggested Reading

- Introduction to the superior colliculus (SC):  
A.J.King, “The Superior Colliculus,” *Current Biology*, vol. 14:R335-R338, 2004. doi:10.1016/j.cub.2004.04.018
  - Useful to give you a general grasp of what the SC is and how it operates
- An example of the detail (less accessible):  
L. Yu, B.A. Rowland, and B.E. Stein, “Initiating the Development of Multisensory Integration by Manipulating Sensory Experience,” *Journal of Neuroscience*, vol. 30(14):4904-4913, 2010. doi:10.1523/JNEUROSCI.5575-09.2010
  - A recent in-depth study on the development of multisensory integration in the SC

# Key Sources

- Core text:

B. E. Stein and M. A. Meredith. “*The Merging of the Senses*,” A Bradford Book, MIT Press, Cambridge, MA., 1993.

- Fundamental concepts and coverage

- Updated coverage:

G. A. Calvert, C. Spence, and B. E. Stein. “*The Handbook of Multisensory Processes*,” A Bradford Book, MIT Press, Cambridge, MA., 2004.

- Comprehensive state-of-the-art





# Multisensory Processing in the Wild

# Making Sense of Our Senses



- Investigation of sensory processing originally took a **unisensory** approach
  - Clear divisions of hierarchical processing
  - Evident in areas such as LGN to V1, V2, ...
- However, key phenomena allowed us to realise that perception is **multisensory**
  - McGurk-MacDonald Effect [3]
  - Rubber hand effect [5]
  - ...



# McGurk-MacDonald Effect



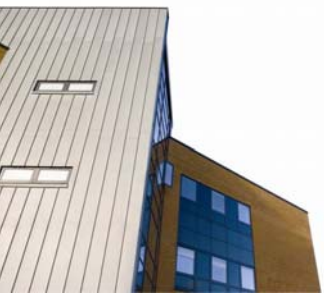
McGurk-MacDonald effect [3]; clip [4]



# Rubber Hand Effect



Rubber hand effect [5]; clip [6]





# Multisensory Phenomena

- McGurk-MacDonald effect [3]
  - Vision alters speech perception
  - Sound /ba/ + visual /ga/ = perception /da/
  - Related to other visually/auditory dominant effects [7]
- Rubber hand effect [5]
  - Interaction between vision, touch and proprioception
  - Perceived the touch of the brush on the rubber hand
  - Related to amputees perception of missing limbs [8]
- Other phenomena include
  - Ventriloquism and synesthesia

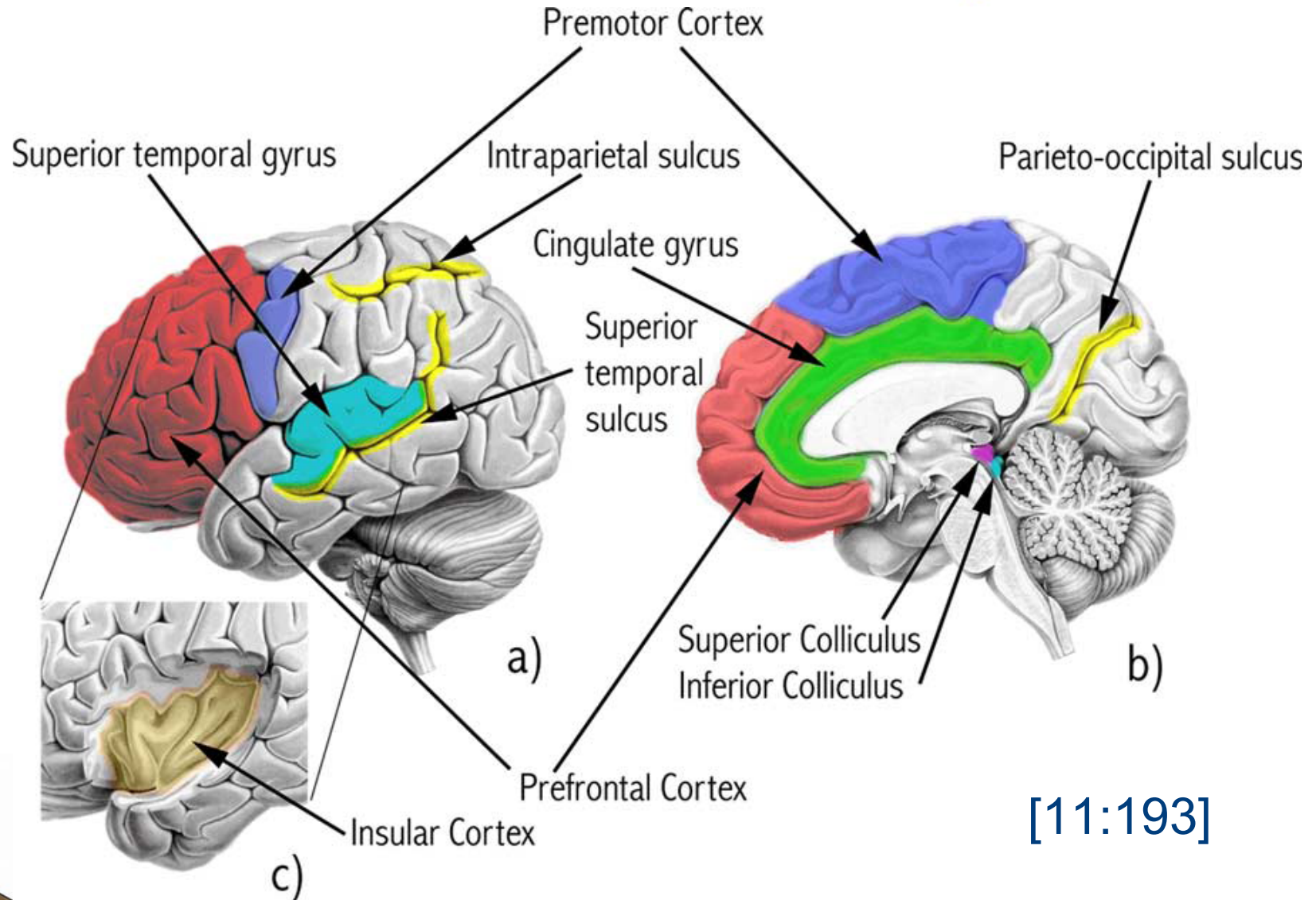
# What is Multisensory Processing?



- Multimodal stimuli are bound if they correspond **spatially** and **temporally**...
  - Two or more stimuli at (approximately) the same space and time [9,11]
  - Even if one stimulus is below normal detection thresholds (think of camouflage)
- ... and with **semantic similarity**
  - McGurk-MacDonald effect [3]
  - Complementary auditory and visual information (lips and speech)



# Extent of Multisensory Processing



[11:193]





# Early vs. Late Processing

- Original convergence studies focused on late stages of cortical processing
  - Association cortical areas
- Now clear that multimodal integration occurs in both **early** and **late** stages [11]
- Structures with convergence include:
  - Midbrain: superior colliculus, thalamus
  - Amygdaloid complex
  - Early auditory cortex → early visual cortex, ...
  - ...



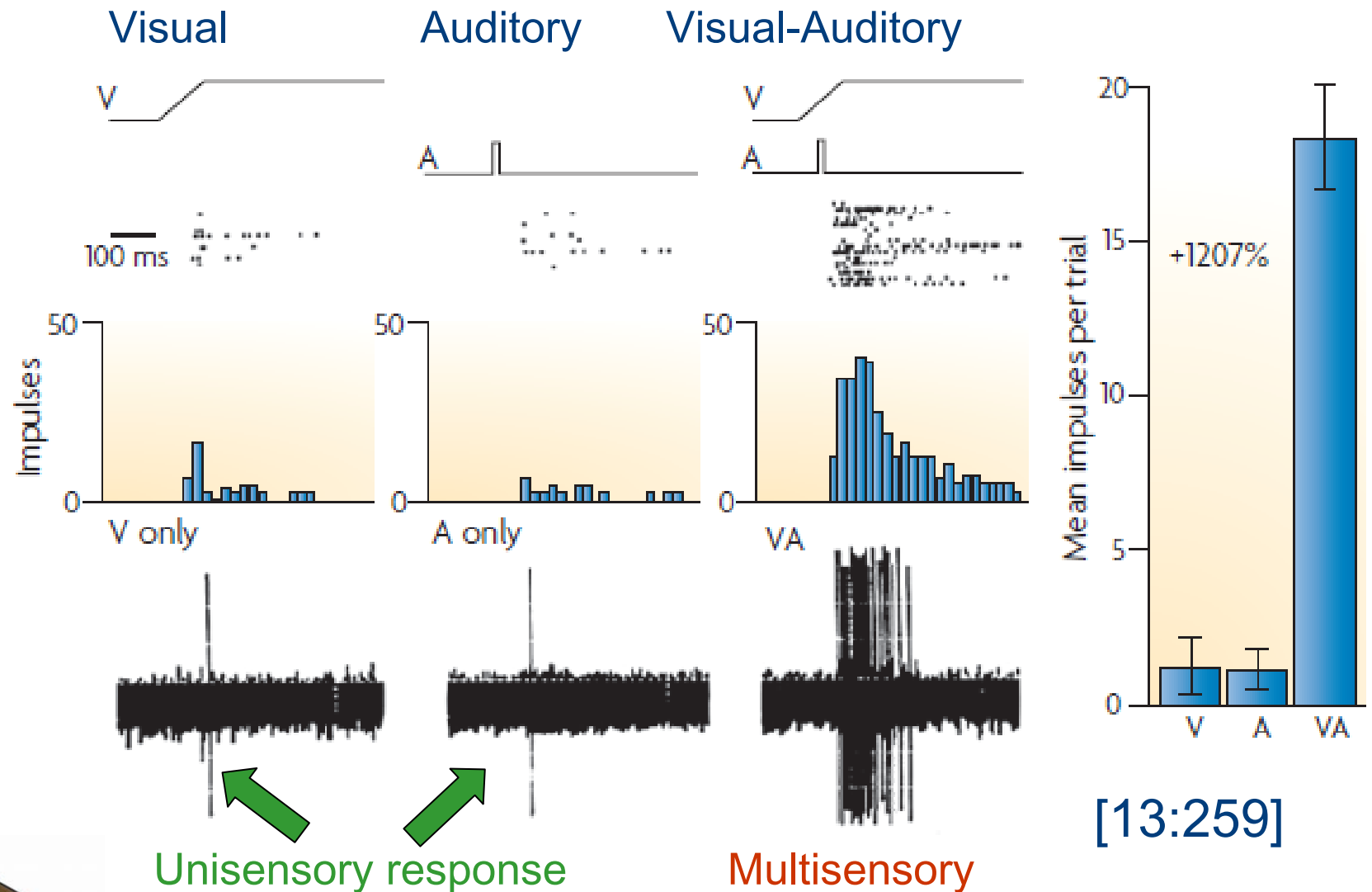
# Neural Mechanisms

- Wide forms of connectivity [12]:
  - Feedforward: combining senses up the hierarchy
  - Feedback: feeding back sensory information
  - Lateral projections: between neurons/regions
- Is multisensory processing fundamentally different to unisensory processing?
  - Not fully understood, but **superadditive** responses [13]
  - Multimodal stimuli provoke **greater responses** than the addition of their **individual unisensory responses**





# Multisensory Neuron



[13:259]



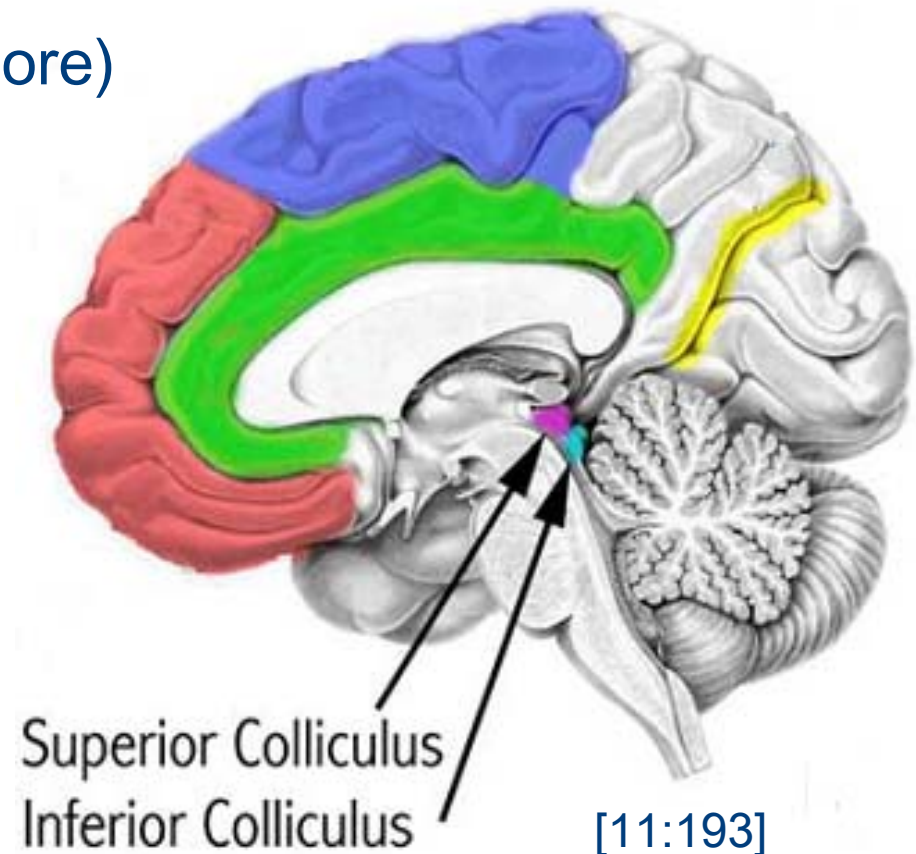


# An Example of Multisensory Processing: Superior Colliculus

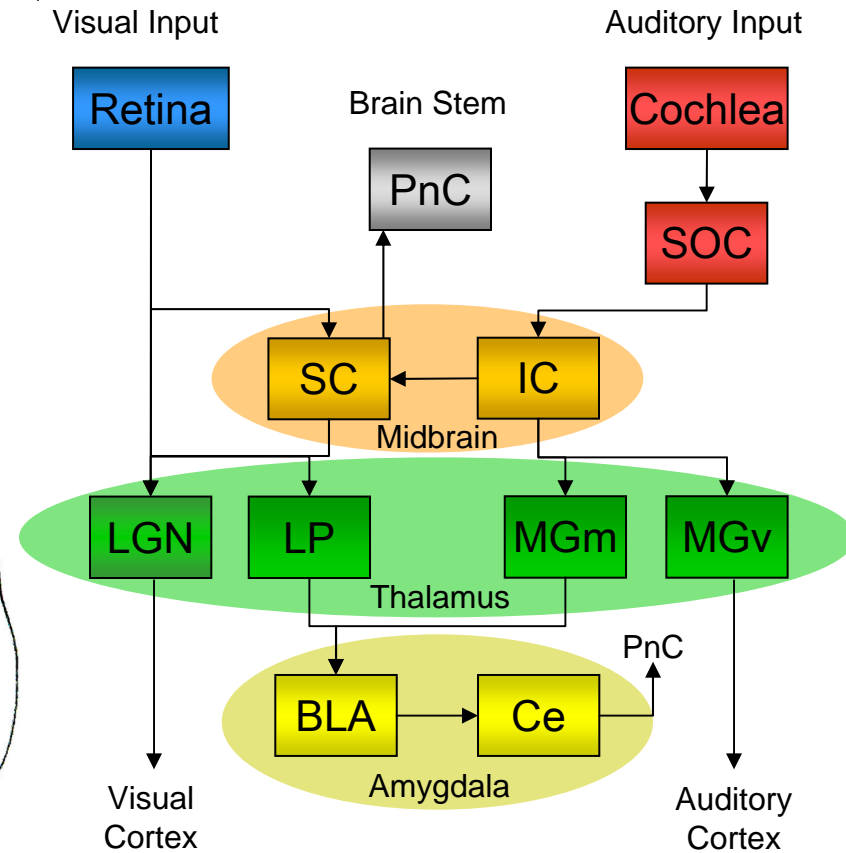
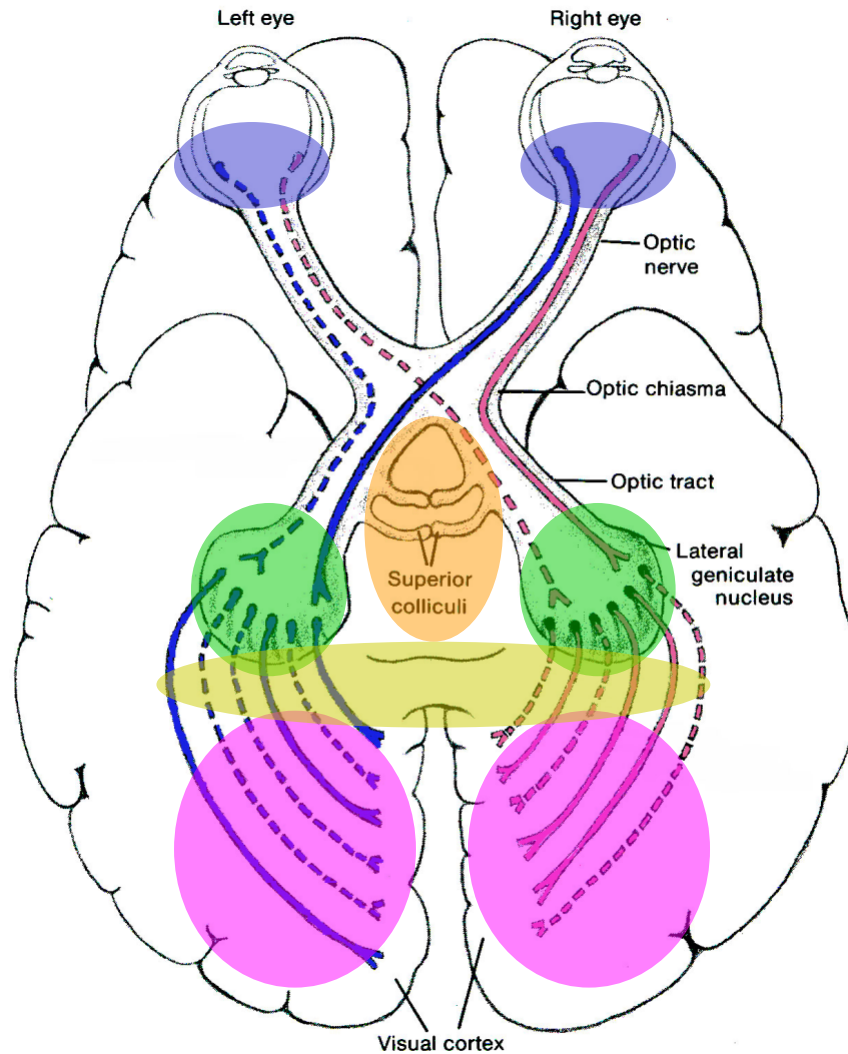
# Subcortical Multisensory Processing



- Stein and colleagues
  - (cf. [2,9,13] and many more)
  - Systematic studies of multisensory processing
  - Cats and rats
- Superior colliculus
  - Gaze shift: seeing, hearing and touch
  - Pivotal role in saccadic system (10 structures)



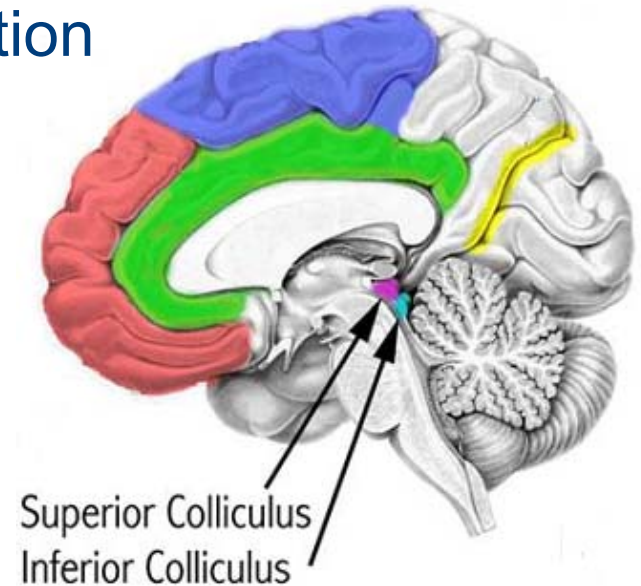
# Audio-Visual Subcortical Function



Constructed from [15,16,17,18]

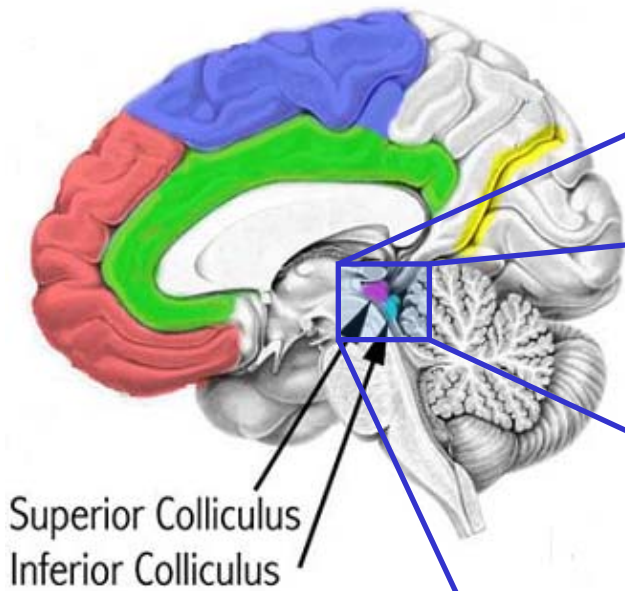
# Superior Colliculus

- Laminated midbrain structure [1,9]
  - Combines visual, auditory and somatosensory stimuli
  - Sensory alignment of topographic maps
  - Forms a multisensory representation
- Causes gaze shifts
  - Prioritises to multimodal stimuli
  - Enhancement and suppression
- Integration is moderated
  - Cortical feedback [19]
  - Unisensory co-operation [20]?

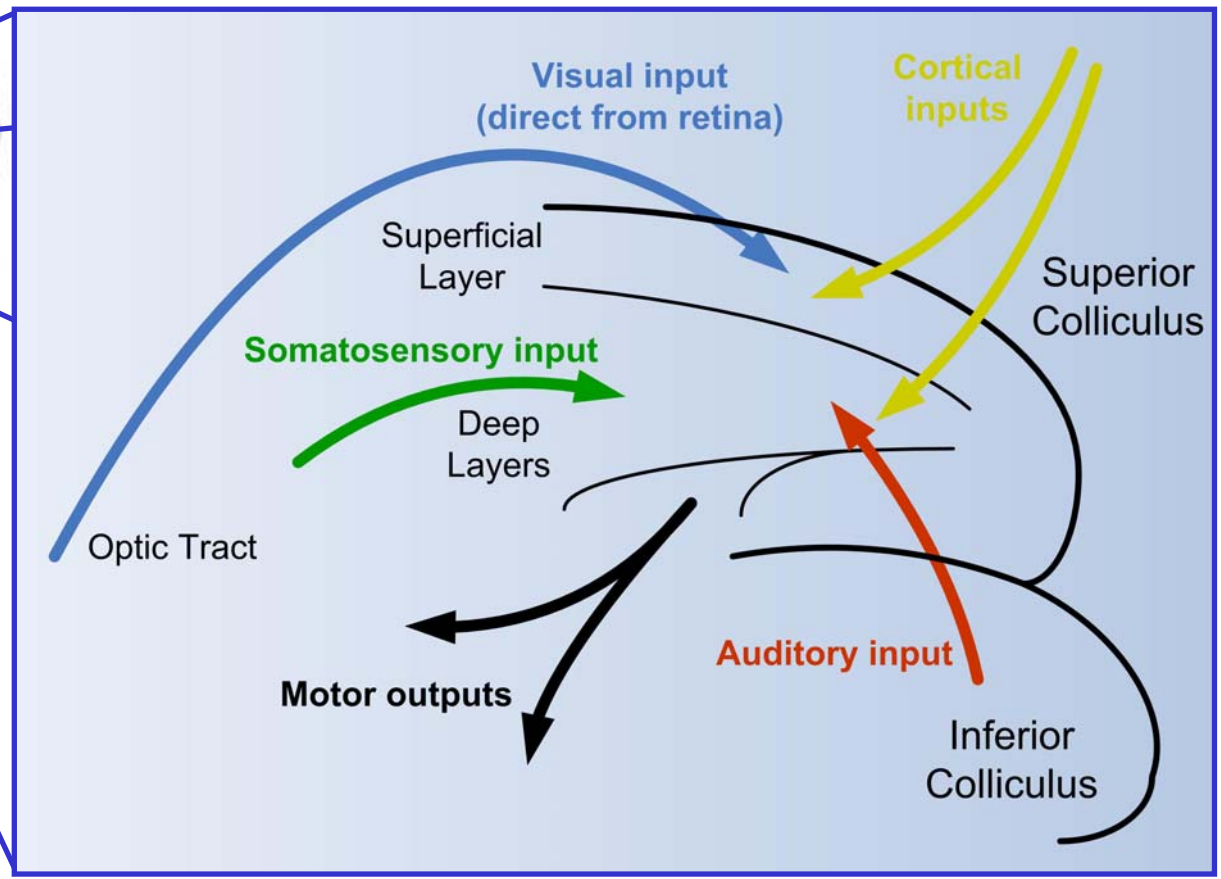


[11:193]

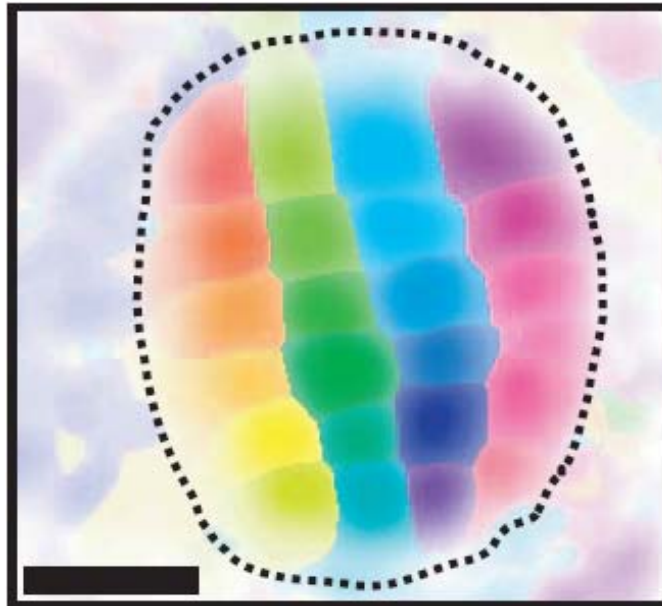
# Superior Colliculus



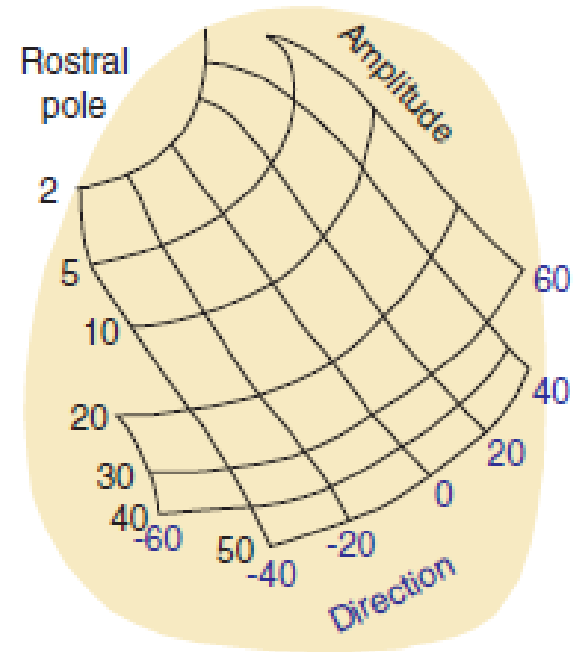
[11:193]



# Topographic Maps



Visual map in the SC of a rat [22]



Deep layer nucleus stimulation in primate – amplitude and direction of eye movement [1]



# Developing Sensory Alignment



- Vision is thought to dominate alignment
  - Correlating visual and auditory stimuli [1]
- Neuronal integration
  - Develops in the first few months post natal
  - Develops autonomously
  - Without being alert or through reward [2]
- Representations [1]
  - All appear to be eye-centred (not body-centred?)
  - Different spatial extents to senses
  - Allows for consistent output to motor organisation
  - Ongoing alignment between maps and output

# Integration and Feedback

- Multisensory integration
  - **Enhancement** of stimuli occurring at the same location and time [9,11]
  - **Suppression** if multiple unimodal stimuli
  - Response is **superadditive** [13]
  - Different circuitry for uni- multi-modal processing [21]
- But, this integration relies upon cortical feedback
  - Visual, auditory and somatosensory areas
  - Unisensory cortical co-operation
  - No co-operation, no enhancement [20]





# What have we learnt from the SC?

- Multisensory integration in the SC
  1. Develops autonomously post natal
  2. Using correlated multimodal stimuli
  3. Appears to be driven by one sense (vision)
  4. Dependent spatial representations (eye-centred)
  5. Superadditive response to multimodal stimuli
  6. Co-operative cortical feedback needed for integration
- How does that help computationally?





# Computational Principles of Multisensory Processing

# Principles of the Superior Colliculus



- Computational models of the SC
  - Provide insights into neuroscience...
  - ...and opportunities for exploitation
- Different types of model have been developed
  - Physiologically motivated models
  - Computational paradigms
  - Larger scale behavioural models
- Explore a wide range of issues
  - But a recent theme has been on developing integration and assessing how this is controlled through cortical feedback





# Previous Models

- Physiologically motivated models focusing on saccades
  - Parallel pathways between SC and cerebellum [23]
  - Combination of senses **competitively** [24]
  - Trajectory information encoded in outputs [25]
  - Integration [30]
  - ... and for antisaccades [26]
- Computationally motivated paradigms
  - Enhancement and suppression [27,29]
- Behavioural models
  - Integration with **competitive** learning [28]
  - Integration with **Hebbian** learning [31,33]
  - Integration with **Hebbian** learning and feedback [32]

Association  
(Hebbian and  
competitive learning)  
matches the  
biological evidence



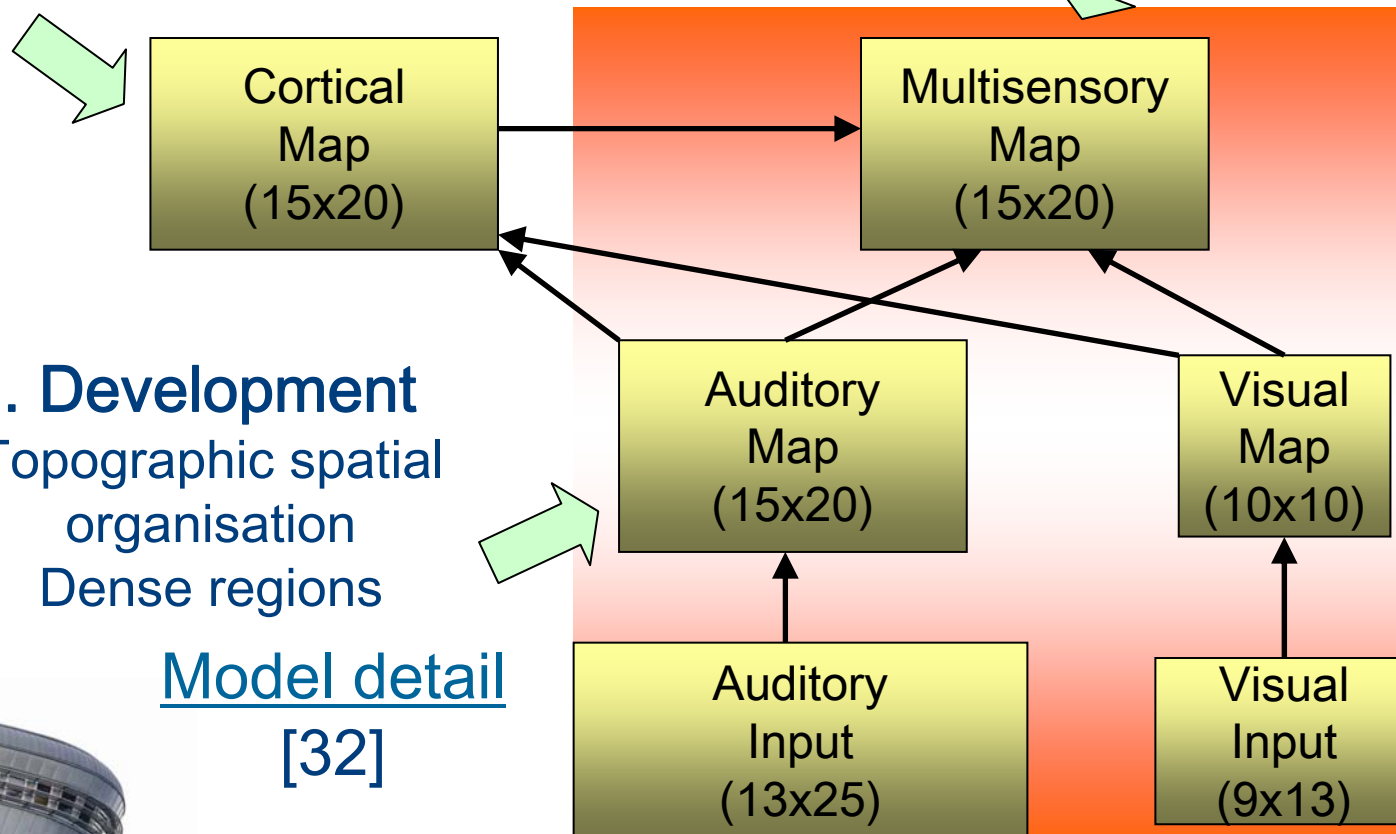
# Example Associative Model

**3. Feedback**  
Enhancement and  
suppression

**2. Integration**  
Coordinate alignment

**1. Development**  
Topographic spatial  
organisation  
Dense regions

Model detail  
[32]

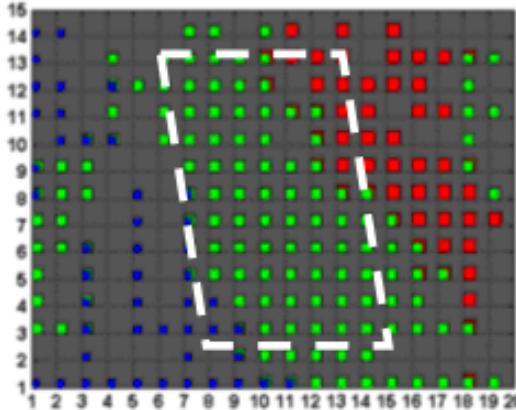


# 1. Spatial Organisation

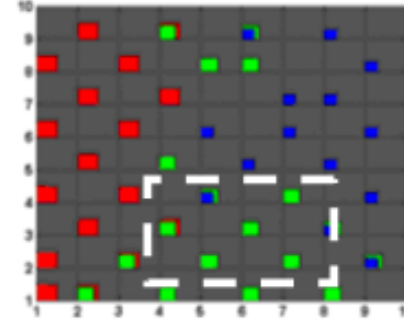
Auditory Map  
Maximum Output Locations

Visual Map  
Maximum Output Locations

- Azimuth: [-180, 180] Elevation: [-90, -45]
- Azimuth: [-180, 180] Elevation: [-30, 30]
- Azimuth: [-180, 180] Elevation: [45, 90]

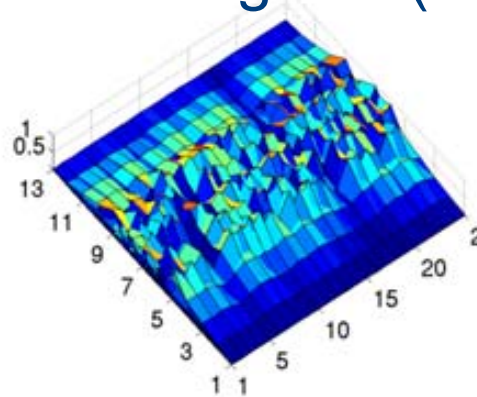


- Azimuth: [-90, -30] Elevation: [-65, 55]
- Azimuth: [-15, 15] Elevation: [-65, 55]
- Azimuth: [30, 90] Elevation: [-65, 55]

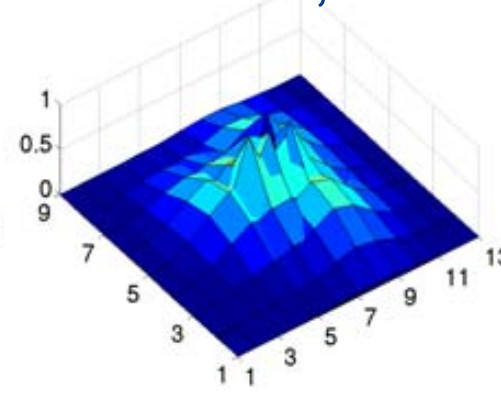


Testing on different examples shows spatial representation  
Larger dense regions (52% vs. 39%; 15% vs. 7%)

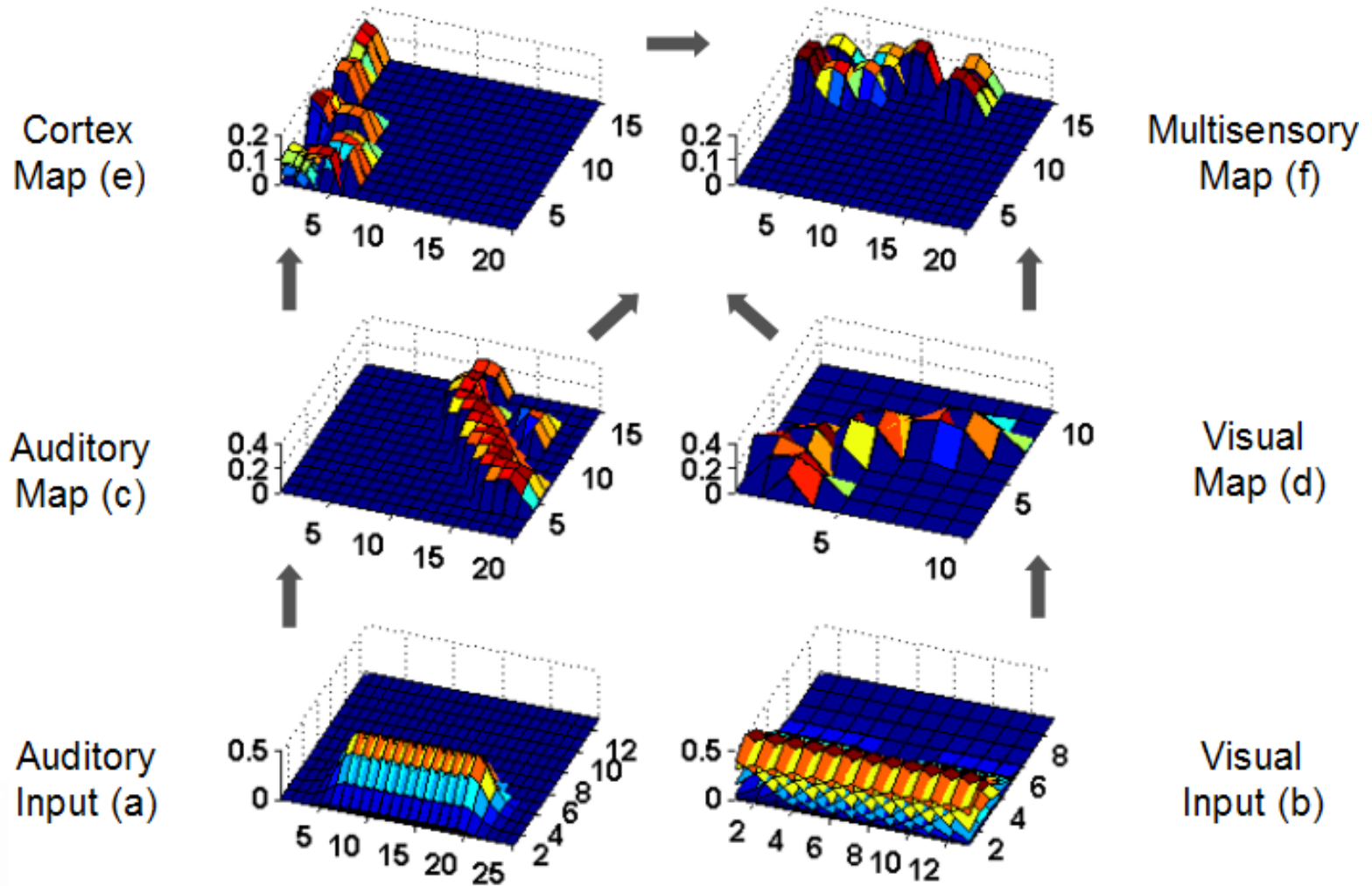
Example Auditory Inputs within  
Azimuth [-180, 180]  
Elevation [30, 30]  
(Dense Area)



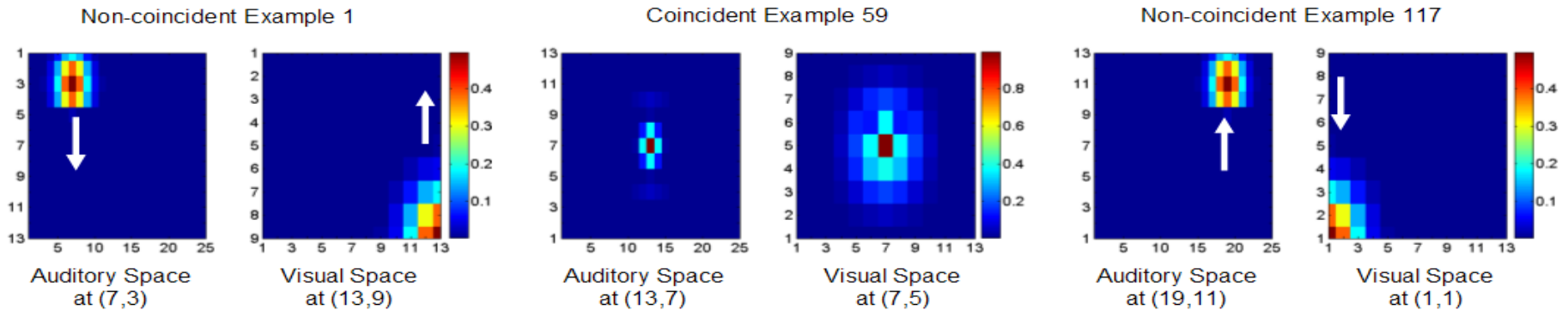
Example Visual Inputs within  
Azimuth [-15, 15]  
Elevation [-15, 15]  
(Dense Area)



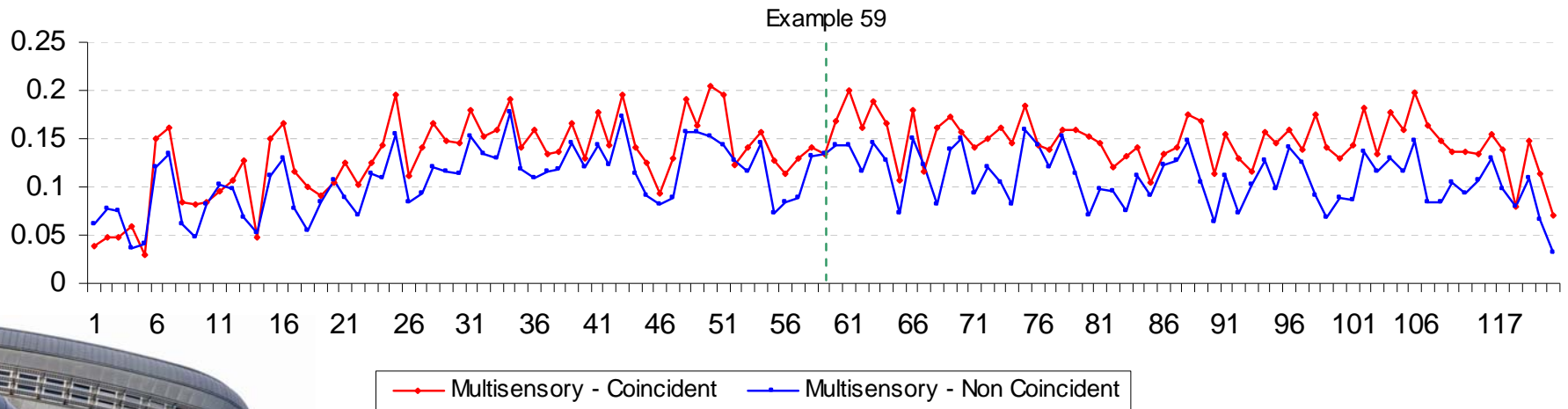
# 2. Coordinate Alignment



# 3. Enhancement and Suppression



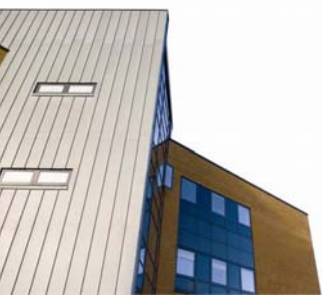
Enhancement: coincident higher activation  
 Suppression: non-coincident lower activation



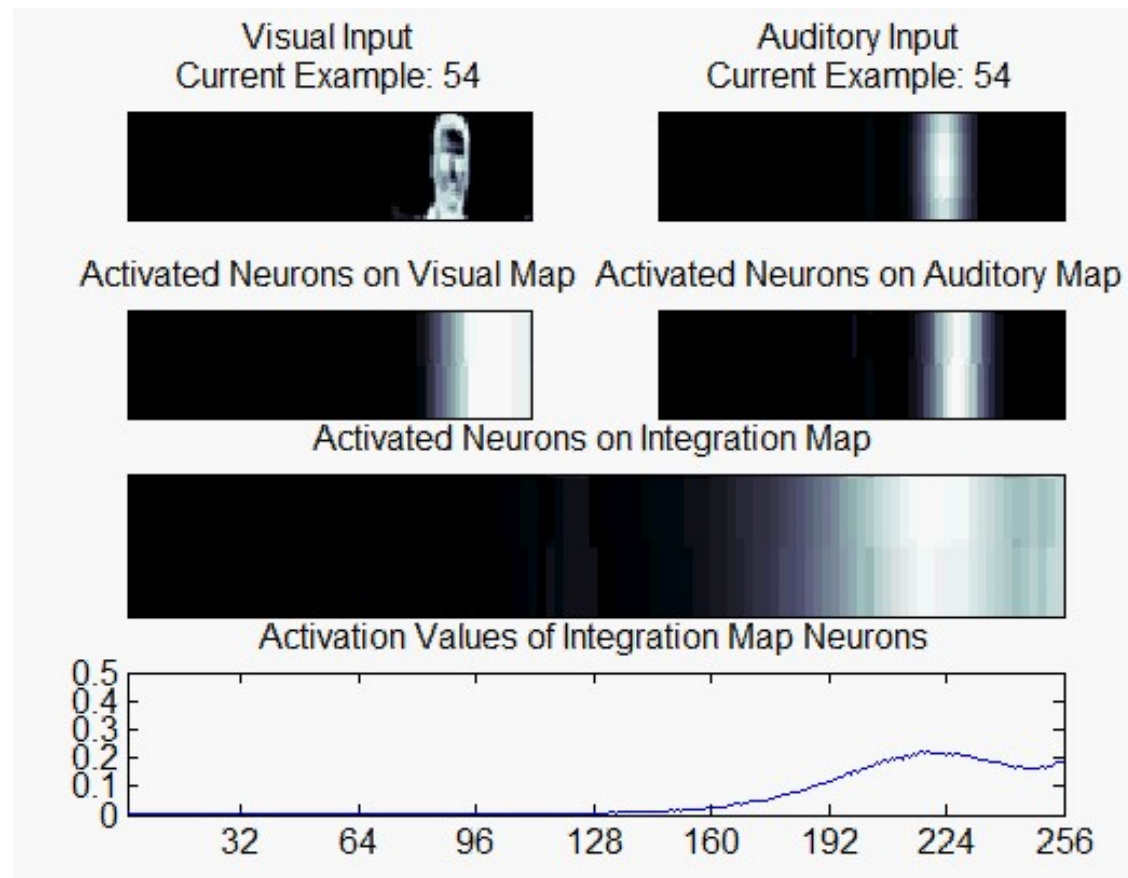
# What have we learnt from models?



- Multisensory integration can be simulated
  1. Development of unisensory representations
  2. Using competitive learning
  3. Co-ordinate alignment of different spatial extents
  4. Into a single multisensory representation
  5. Enhanced multimodal responses
  6. Simple cortical feedback for enhancement
- And it can be applied to practical problems...



# Computational Exploitation



## Real-time visual and auditory integration:

- Rapid facial localisation
- Sound localisation (interaural level difference)
- Integration: real-time speaker localisation



# Conclusion



# Summary

- Sensory processing in the brain
  - Is both **unisensory** and **multisensory**
  - Multisensory integration develops **autonomously**
  - Spatially and temporally coincident stimuli
  - Semantically similar stimuli
- Models have been developed to simulate this
  - Demonstrating **possible methods** (association)
  - But they require examples of **coincidence**
  - May be **time consuming** to construct (computational complexity)
  - And they have not been tried on **complex stimuli**





# Questions

- Do we know enough about neuronal integration to apply this successfully in computational systems?
  - We have a very good understanding of the SC
  - Is this sufficient?
- Can EEG, MEG, fMRI, MRI, DWI and/or PET data be combined automatically using such associative techniques?
  - Association appears to provide automatic registration of co-ordinate systems on simple data
  - Can it work for more complex and temporal data?



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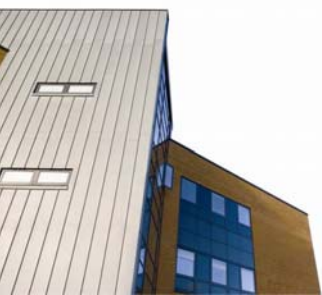
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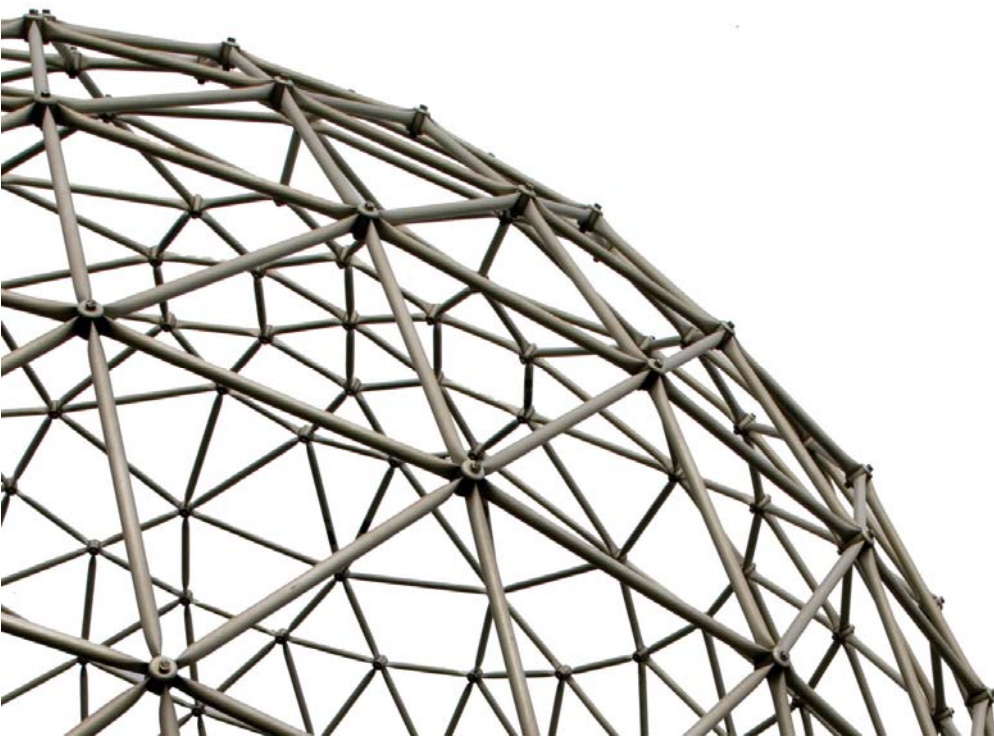


Thank you

Questions?

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# Abstract



Our ability to rapidly process and act upon sensory information is an important animal attribute. While sensory processing is often considered to occur in isolation to other senses, this unisensory view of processing has changed over the last 30 years with a growing realisation that multisensory integration at all levels of the brain is important. Pivotal moments in this realisation include the discovery of the McGurk-MacDonald effect, which demonstrates how influential vision can be on speech processing; as well as oddities such as the rubber hand effect. Systematic studies of multisensory integration have provided insight into how brain structures develop and use multimodal stimuli. Such studies are exemplified by the superior colliculus (SC), which is the subcortical structure responsible for shifting our gaze to focus on prominent stimuli regardless of which sense the stimulus was detected in. In this hot topic presentation, I will provide a brief overview of some of the phenomena that demonstrate our multisensory capability. By way of example, I will then focus on how the brain integrates vision, audition and touch to shift our gaze in the SC, moderated by cortical feedback. To provide examples of how such integrated processing may help in combining non-invasive brain measurement modalities, to finish off I will explore how some of the principles of the SC relate to computational techniques.

An essential introduction to the superior colliculus (SC) for all attendees is the “primer” article by King:

A.J.King, “The Superior Colliculus,” *Current Biology*, vol. 14:R335-R338, 2004. doi:10.1016/j.cub.2004.04.018

This explains the role of the SC, including how the senses are combined.

For attendees who wish to look closer at the detail of multisensory integration and the current forefront of our knowledge, then try the following (less accessible) article:

L. Yu, B.A. Rowland, and B.E. Stein, “Initiating the Development of Multisensory Integration by Manipulating Sensory Experience,” *Journal of Neuroscience*, vol. 30(14):4904-4913, 2010. doi:10.1523/JNEUROSCI.5575-09.2010





# Neural Model

- Topographic maps
  - Spatial representation [33]
  - Develops organisation
- Competitive learning
  - Hebbian association [18]
  - Maps trained in layers
- Integration
  - Map outputs as inputs
  - Unisensory → multisensory
  - Cortex → multisensory

Neuron output

$$u_{ij} = \sum_{k=1}^m x_k w_{kij}(t),$$

$$y_{ij} = \begin{cases} f(u_{ij}) & \text{if } \|c_{ij} - c_{win}\| < h(t) \\ f(u_{ij} - y_{win}) & \text{otherwise} \end{cases}$$

$$f(u) = \begin{cases} 1 & u \geq 1 \\ u & 0 < u < 1 \\ 0 & u \leq 0 \end{cases},$$

Weight Update

$$w'_{kij}(t+1) = w_{kij}(t) + \epsilon(t)x_k y_{ij}$$

$$w_{kij}(t+1) = \frac{w'_{kij}(t+1)}{\sum_{l=1}^m w'_{lij}(t+1)}$$

Neighbourhood and learning rate

$$h(t) = r_{min} + (r_{max} - r_{min})e^{-\left(\frac{(t/t_e)^2}{2r_s^2}\right)}$$

$$\epsilon(t) = l_{min} + (l_{max} - l_{min})e^{-\left(\frac{(t/t_e)}{2l_s^2}\right)}$$

