

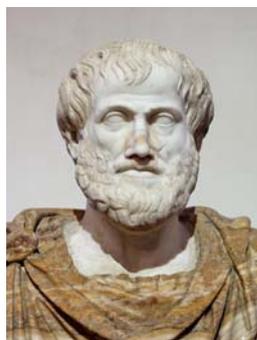
Motion

Andy Rider

a.rider@ucl.ac.uk

Motion aftereffect

- If you stare at something that contains motion, and then look at something that's stationary, you perceive illusory motion in the opposite direction



First described by Aristotle
(384–322 BC)



Then by Lucretius
(99–55 BC)

Motion aftereffect

Addams, R. (1834). An account of a peculiar optical phænomenon seen after having looked at a moving body. *London and Edinburgh Philosophical Magazine and Journal of Science*, 5, 373–4.



Fall of Foyers

https://www.youtube.com/watch?v=6MK9qQ_ApHQ

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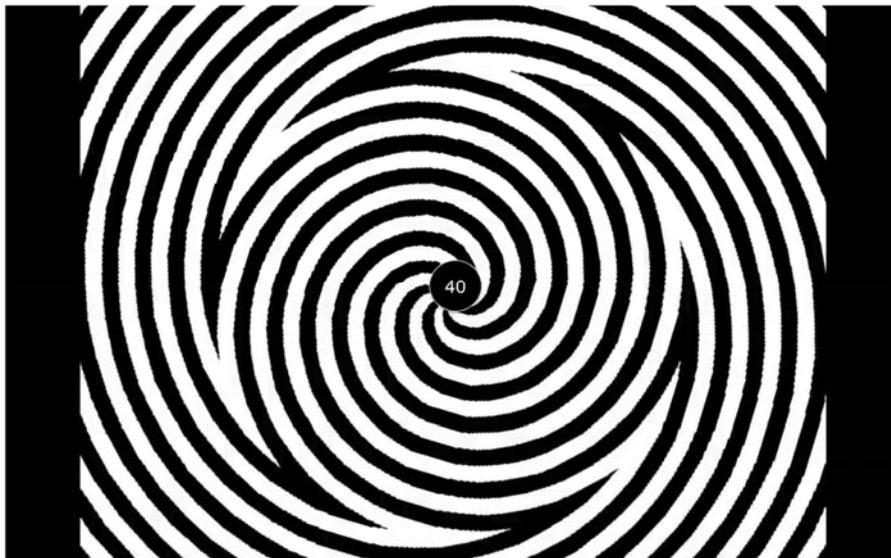
Motion aftereffect



Storm Illusion

<https://www.youtube.com/watch?v=OAVXHzAWS60>

Motion aftereffect



Storm Illusion

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Motion aftereffect

Wohlgemuth (1911)

ON THE AFTER-EFFECT OF SEEN MOVEMENT

by

A. WOHLGEMUTH, D.Sc. (LOND.)

THESIS APPROVED FOR THE DEGREE OF DOCTOR
OF SCIENCE IN THE UNIVERSITY OF LONDON

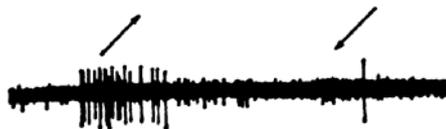
PREFACE

THE research to which the following pages are devoted has been carried out in the PSYCHOLOGICAL LABORATORY, UNIVERSITY COLLEGE (UNIVERSITY OF LONDON), GOWER STREET, LONDON, W.C.

Direction-selective cells in visual cortex



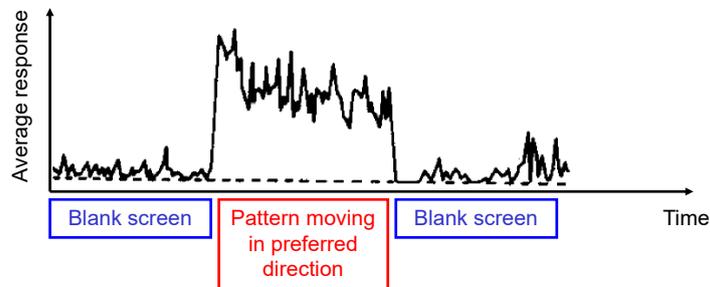
Hubel & Wiesel (1959): Neuron in cat primary visual cortex (V1)



Hubel & Wiesel (1968): Neuron in monkey primary visual cortex (V1)

Adaptation of direction-selective neurons

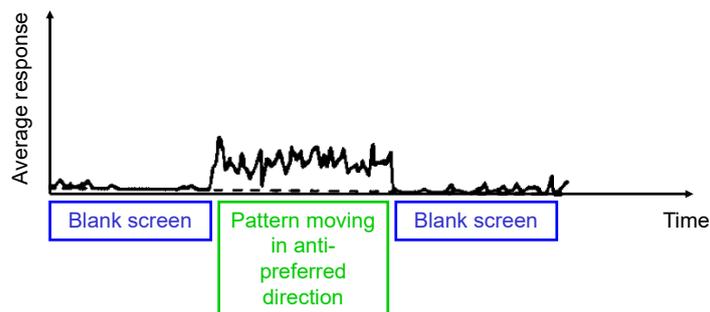
Vautin & Berkley (1977): Neuron in cat primary visual cortex (V1)



- Presentation of motion with neuron's preferred direction causes substantial adaptation

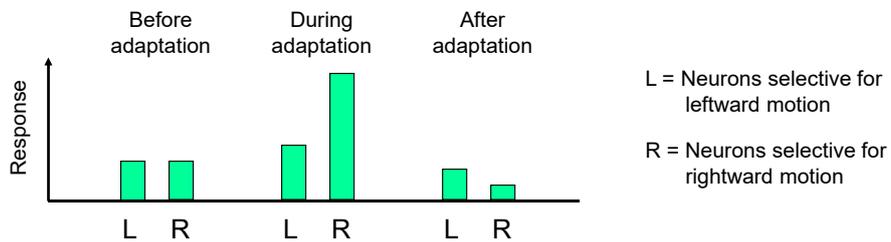
Adaptation of direction-selective neurons

Vautin & Berkley (1977): Neuron in cat primary visual cortex (V1)



- Presentation of pattern with neuron's anti-preferred direction (i.e., opposite to preferred direction) generates a weaker response, and less adaptation
- This suggests that adaptation results from responding strongly

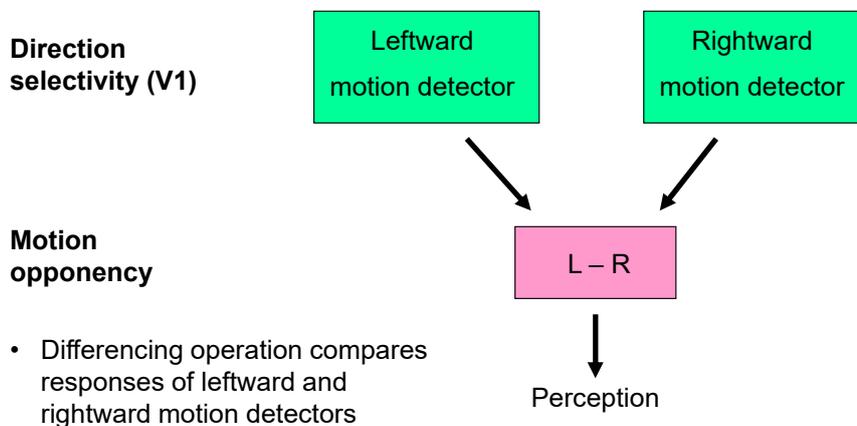
Sutherland's (1961) "Ratio model" of MAE



- Perceived motion direction depends on relative activity of neurons tuned to opposite directions of motion
- Before adaptation, neurons selective for leftward and rightward motion are equally responsive
- Prolonged exposure to rightward motion stimulates rightward-selective neurons more than leftward-selective neurons
- After adaptation, rightward-selective neurons are less responsive than leftward-selective neurons
- Greater response of leftward-selective neurons interpreted as leftward motion

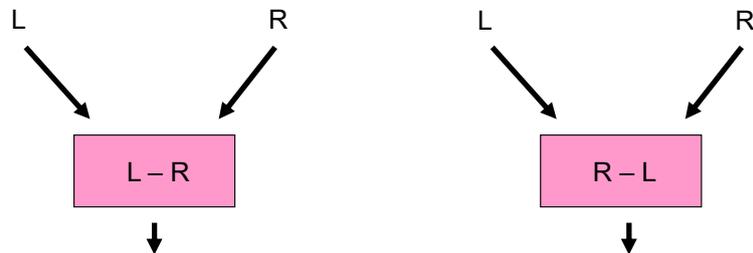
Sutherland's (1961) "Ratio model"

- "the direction in which something is seen to move might depend upon the ratios of firing in cells sensitive to movement in different directions."
- In fact, all modern models of motion perception involve a *difference* between responses of cells selective for motion in opposite directions



Representing negative numbers in the brain

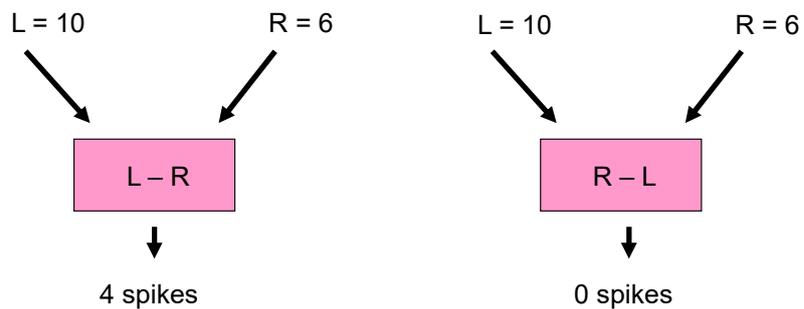
- Do the subtraction both ways



- If the subtraction gives a negative number, the output will be zero
- The $L - R$ unit responds to positive values of $L - R$
- The $R - L$ unit responds to negative values of $L - R$

Representing negative numbers in the brain

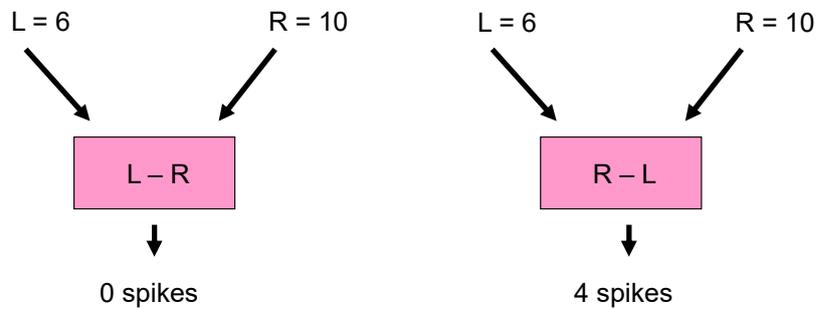
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Representing negative numbers in the brain

- Do the subtraction both ways



- If the subtraction gives a negative number, the output will be zero
- The $L - R$ unit responds to positive values of $L - R$
- The $R - L$ unit responds to negative values of $L - R$
- In models of the brain, it's simpler to let the response values go negative

Outline of model of motion perception

Direction selectivity (V1)

Leftward motion detector

Rightward motion detector

Motion opponency

L - R

Perception

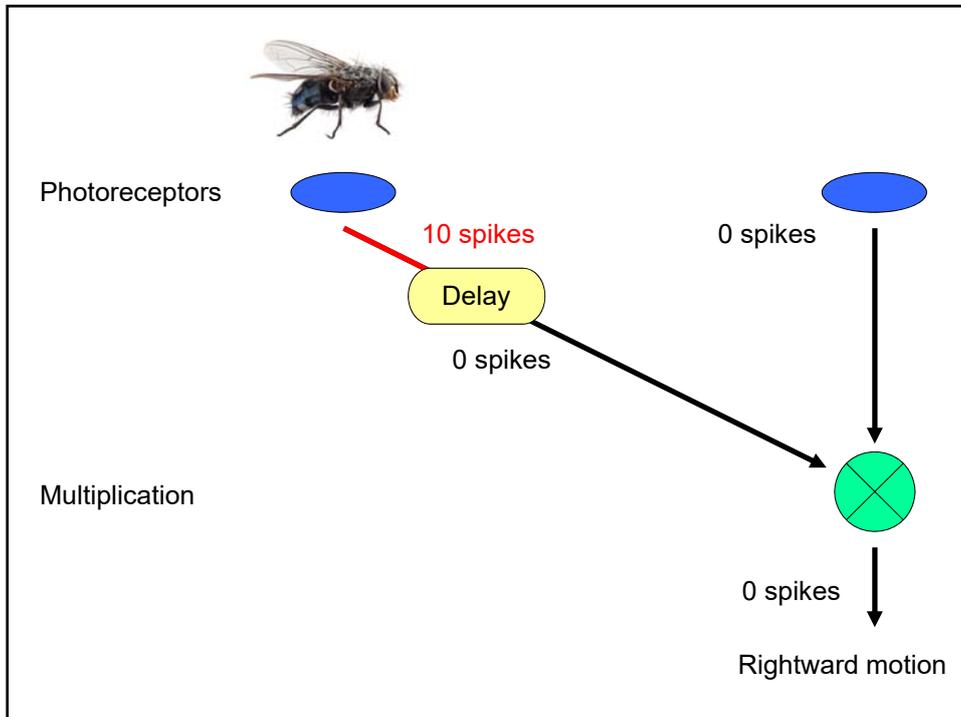
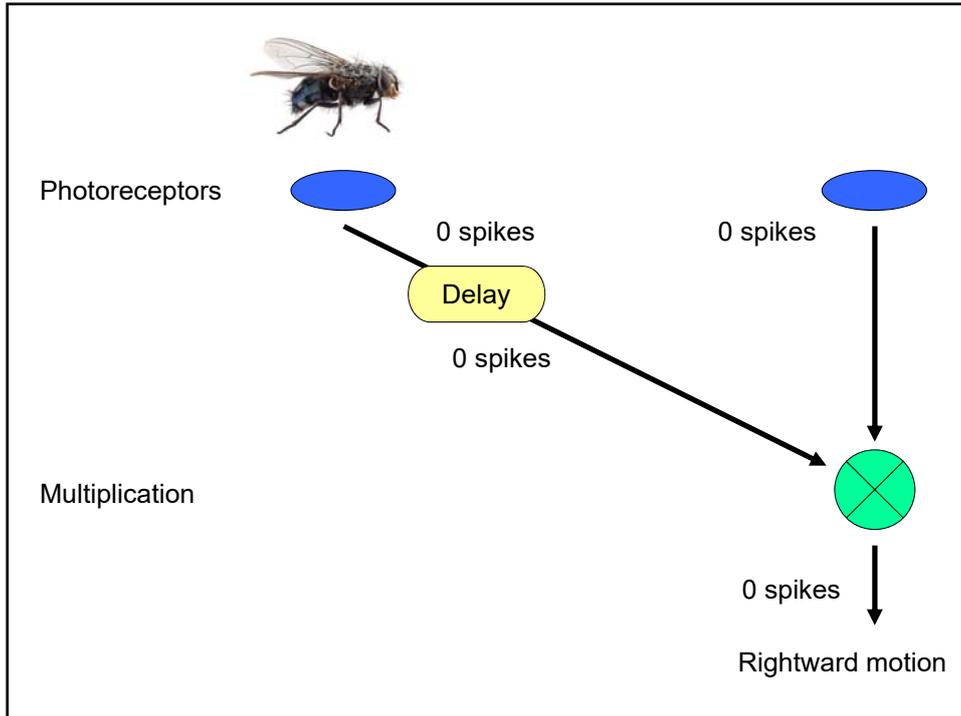
- Not just leftward and rightward motion detectors – opponent pairs tuned to each direction
- How are motion detectors constructed?

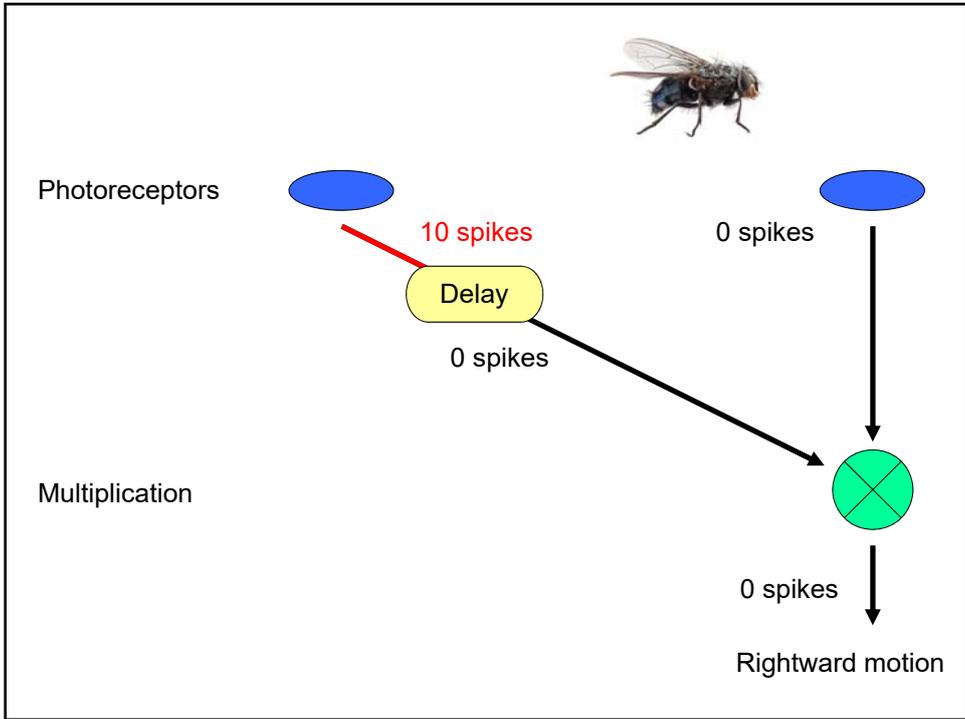
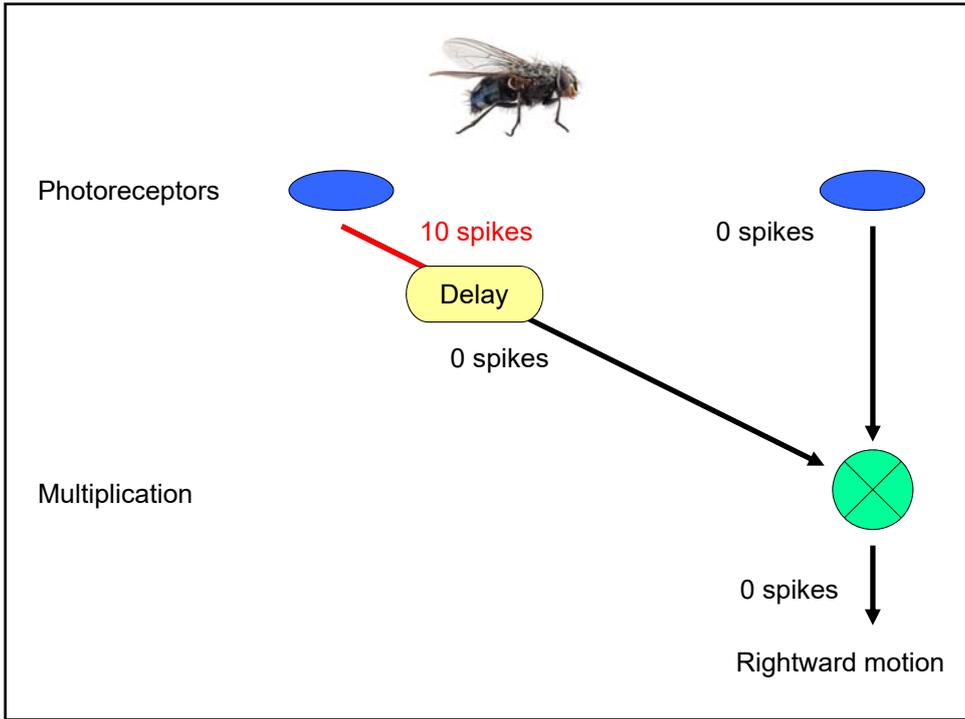
Werner Reichardt

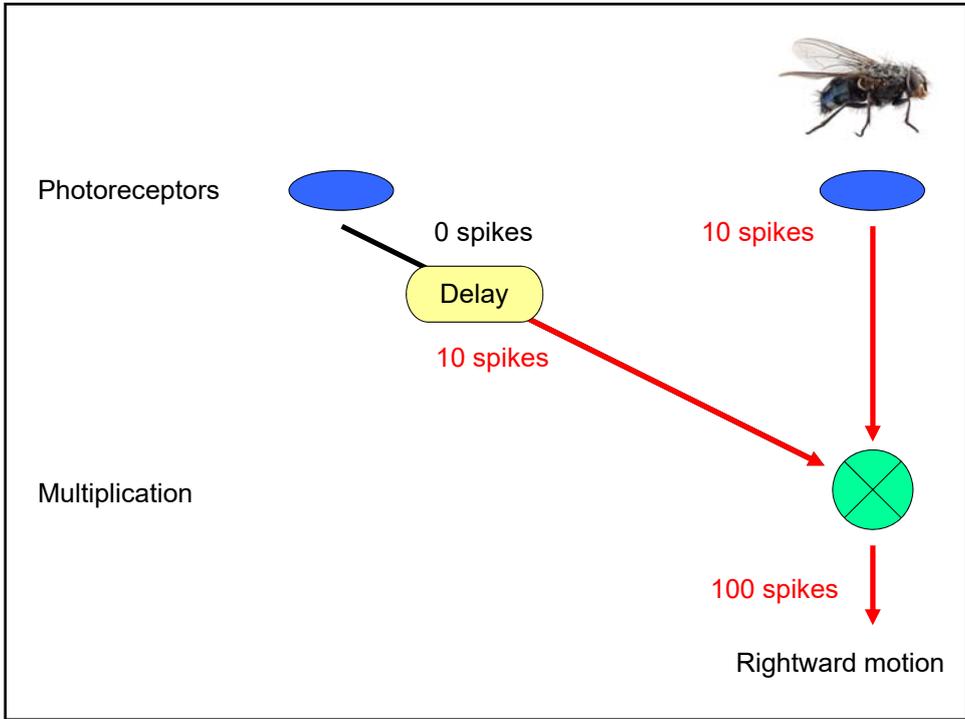
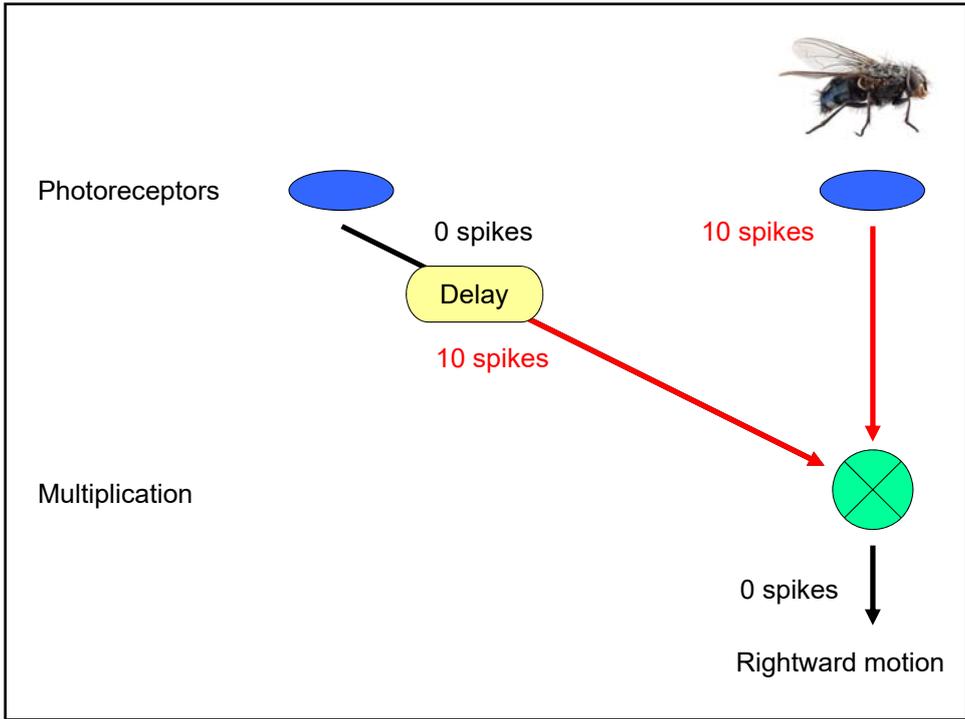
(1924–1992)

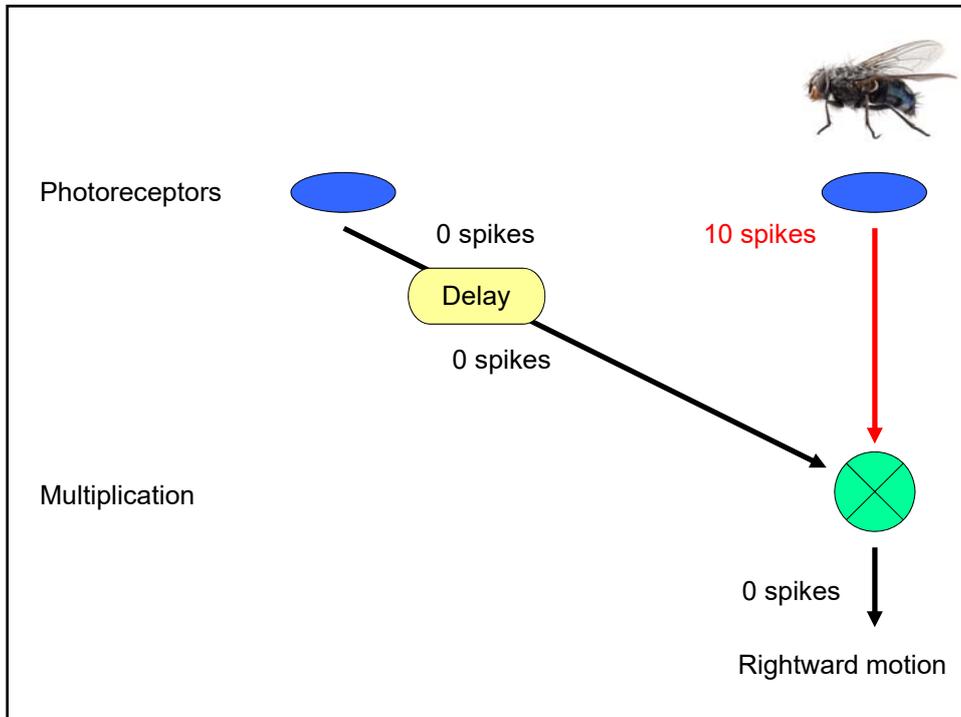
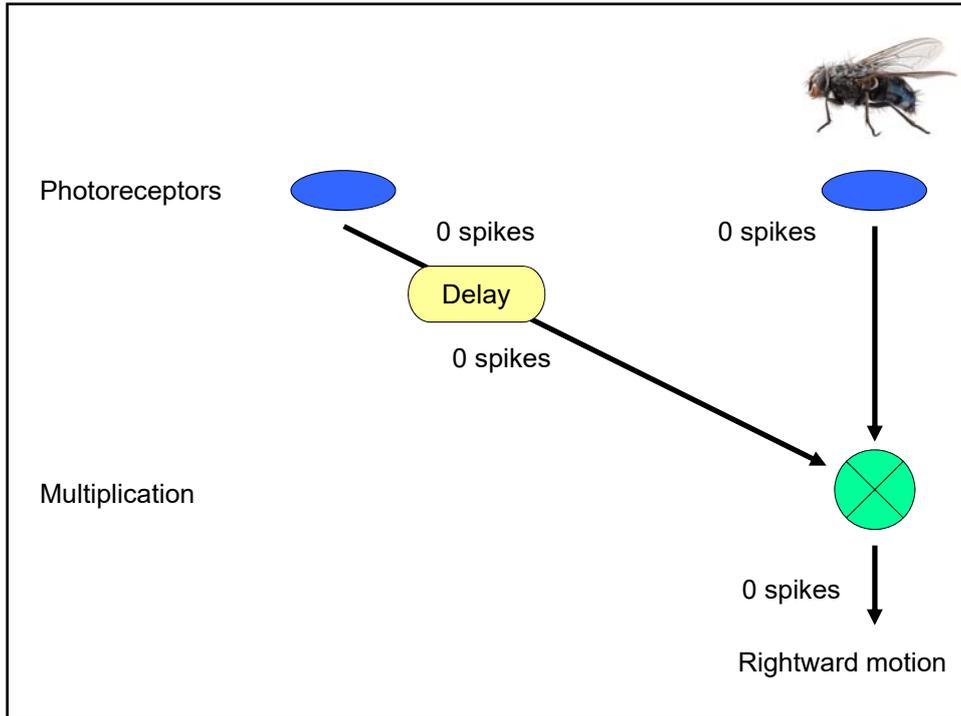
- German Radio engineer
- Pioneered application of engineering principles to neuroscience
- Most famous for developing a model of motion detection in the fly: the “Reichardt detector”

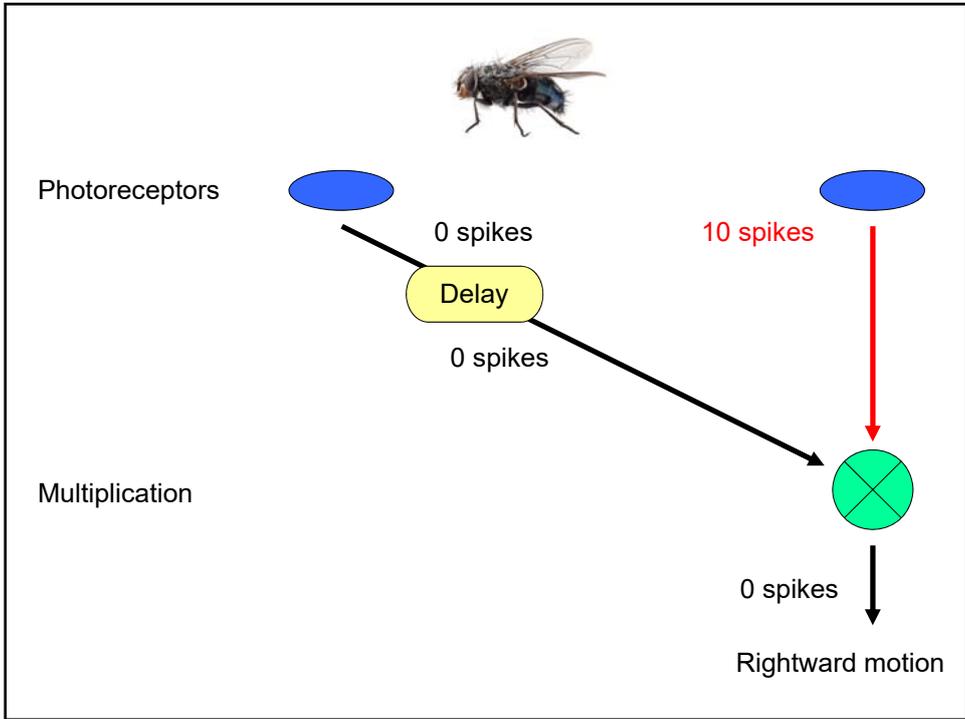
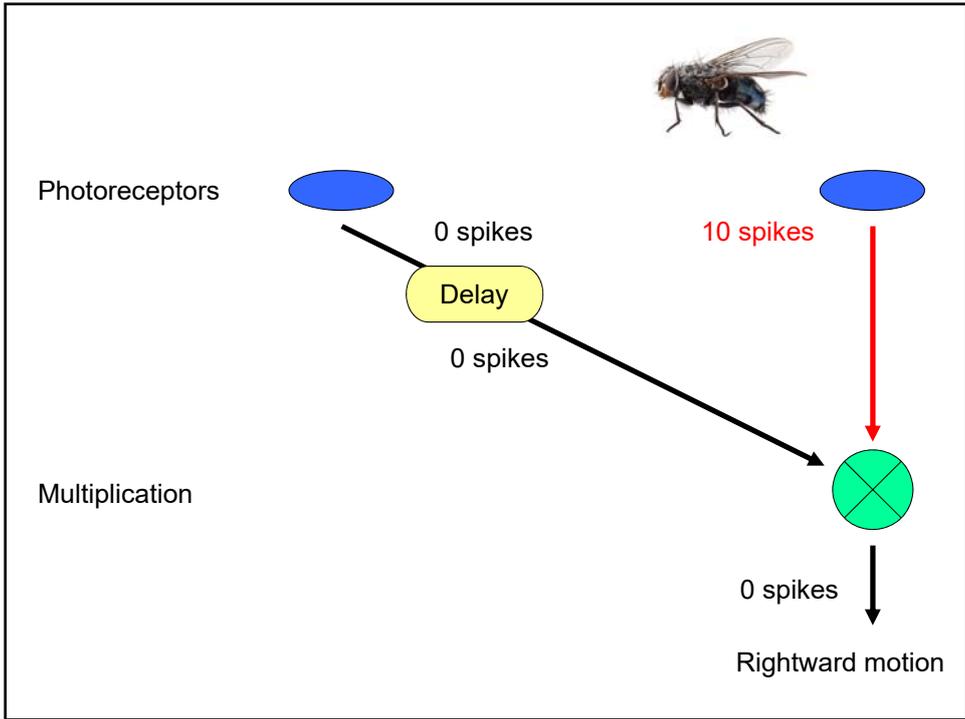


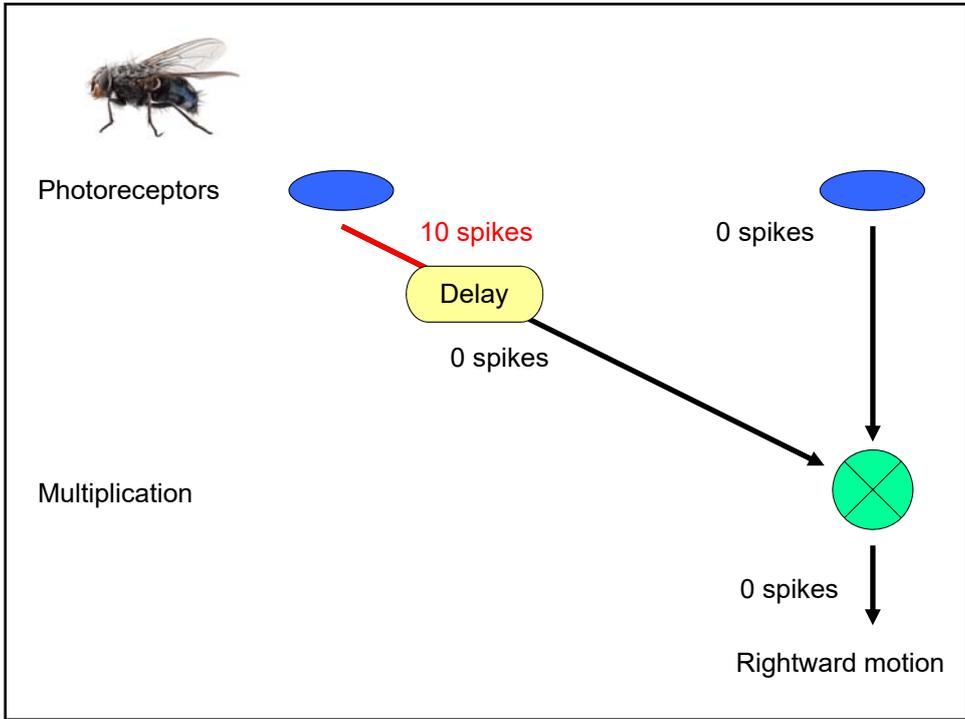
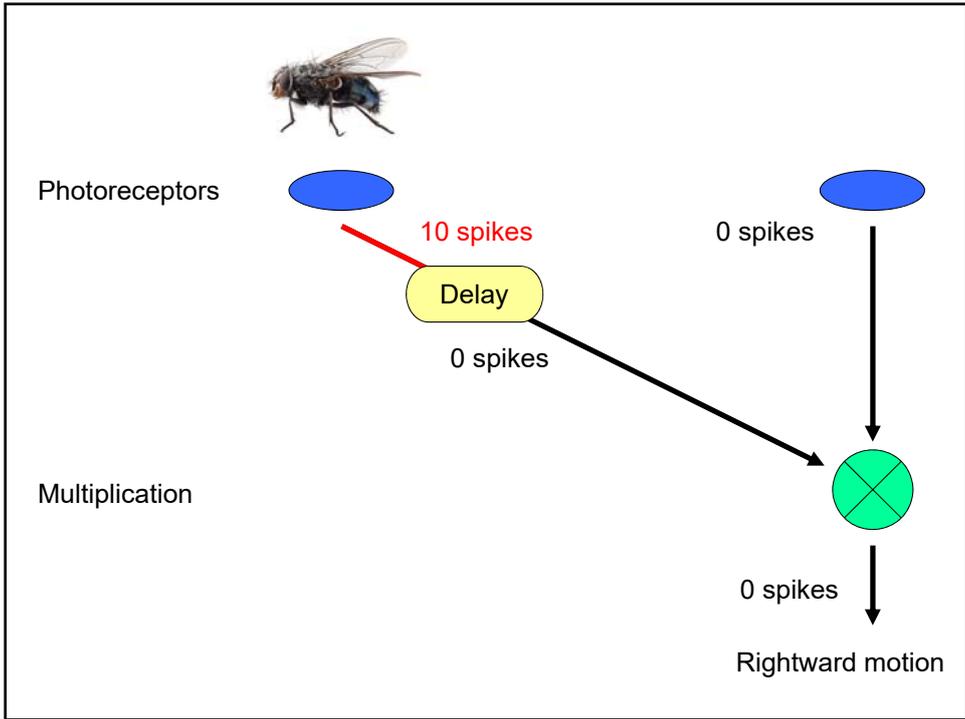


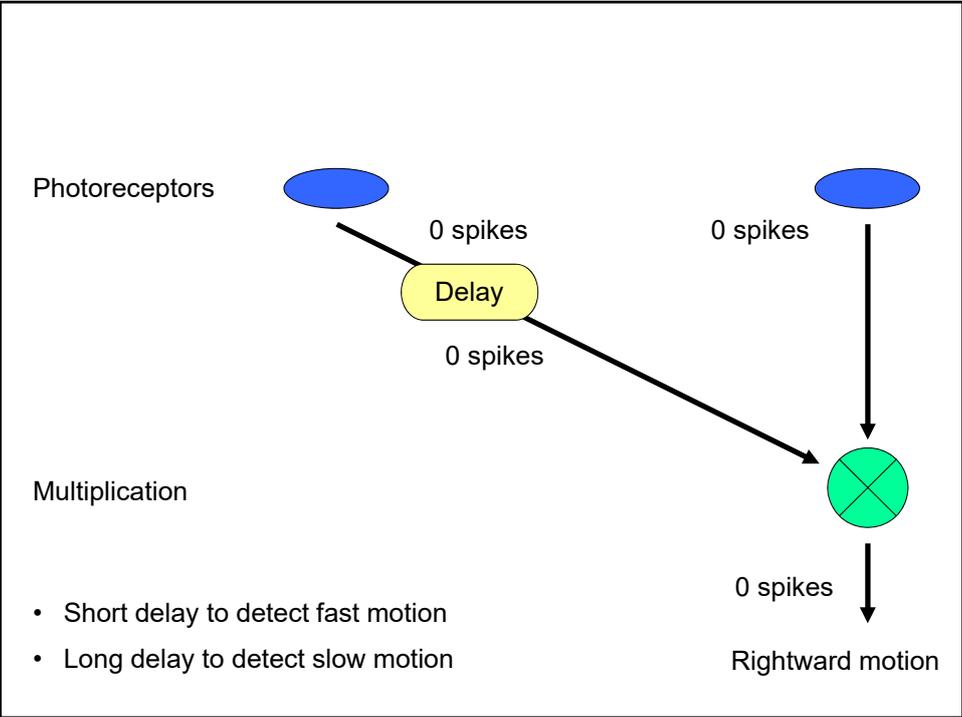
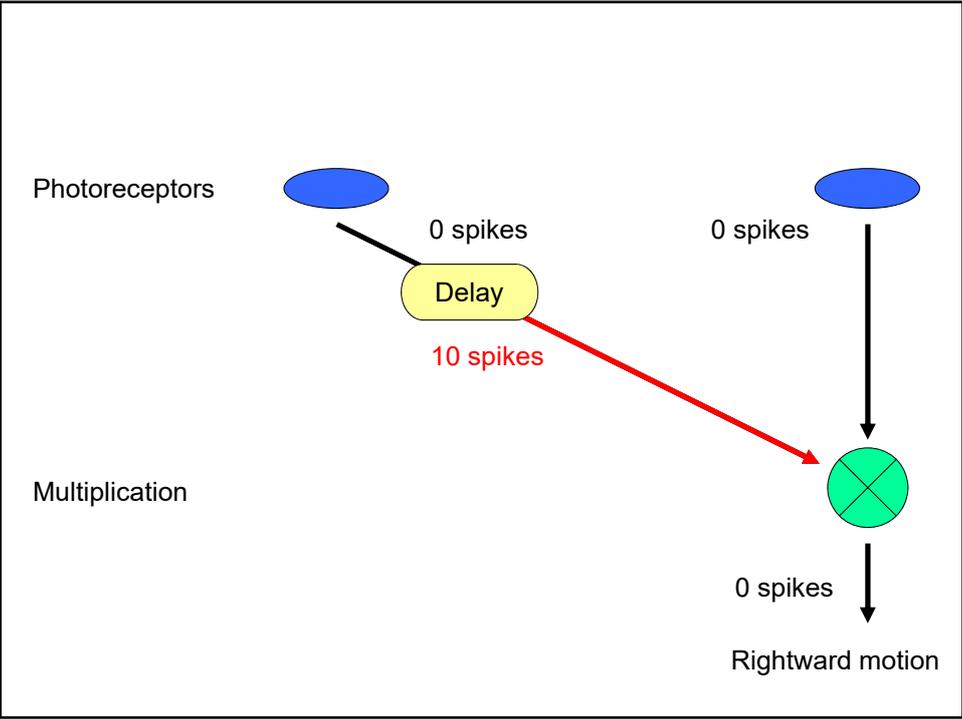


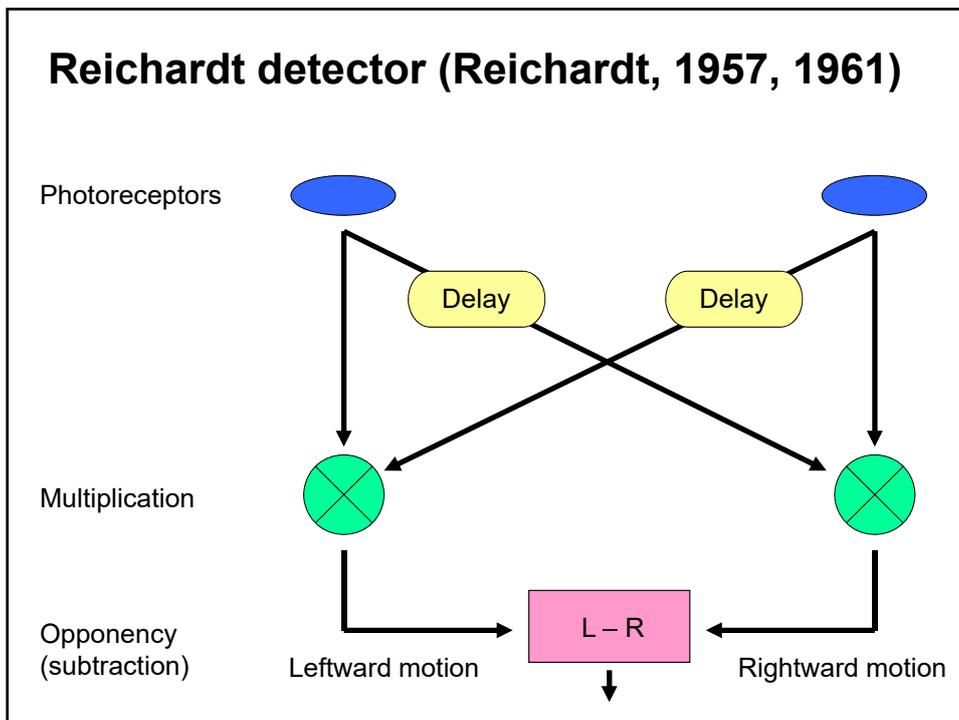
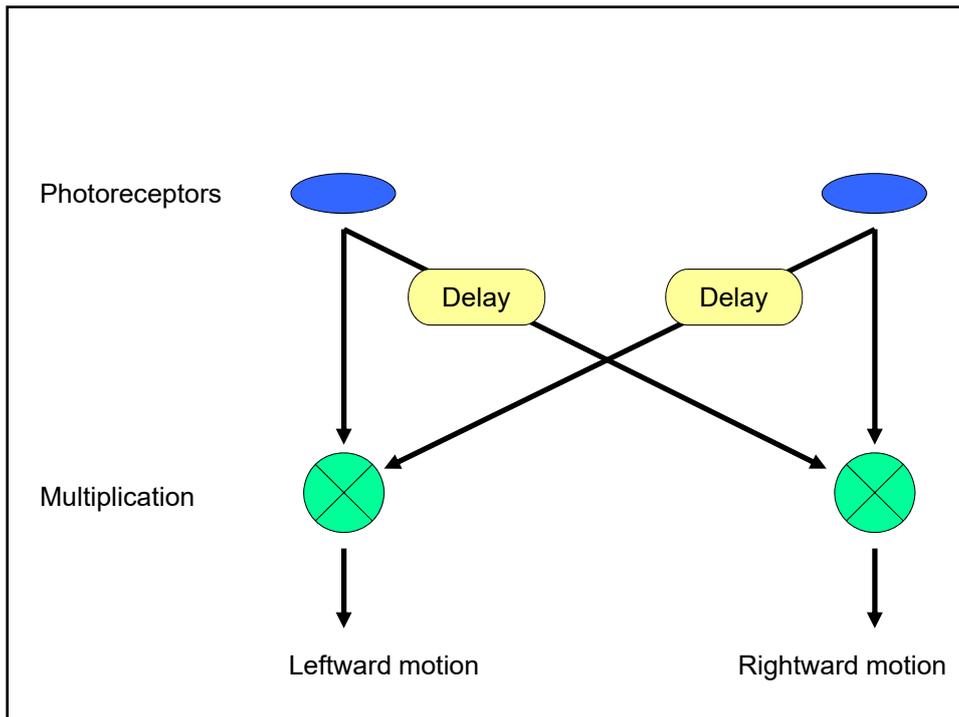








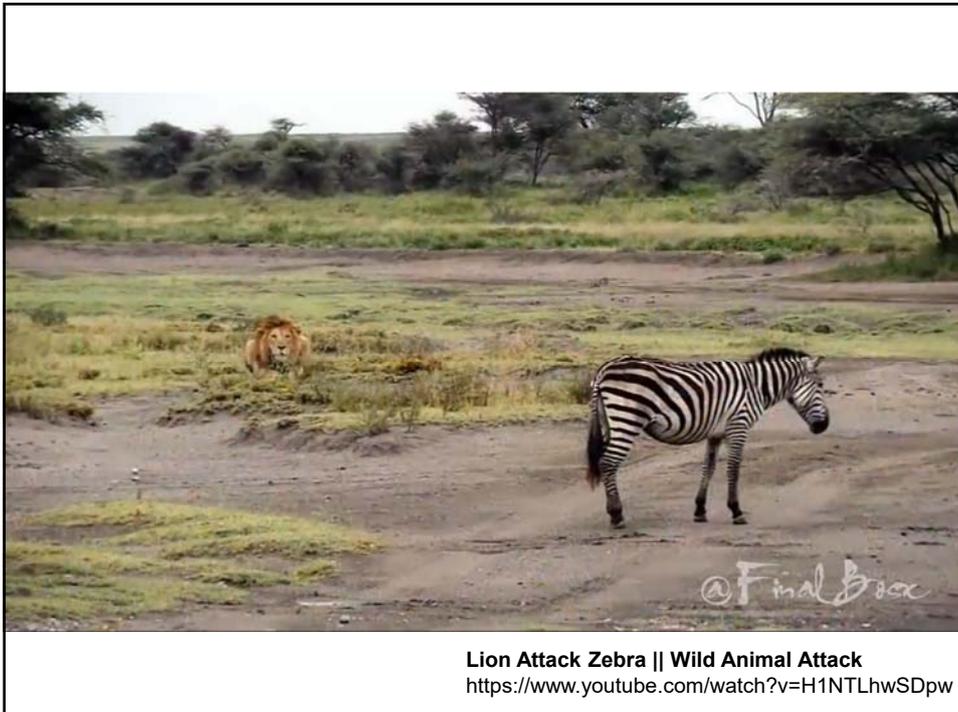






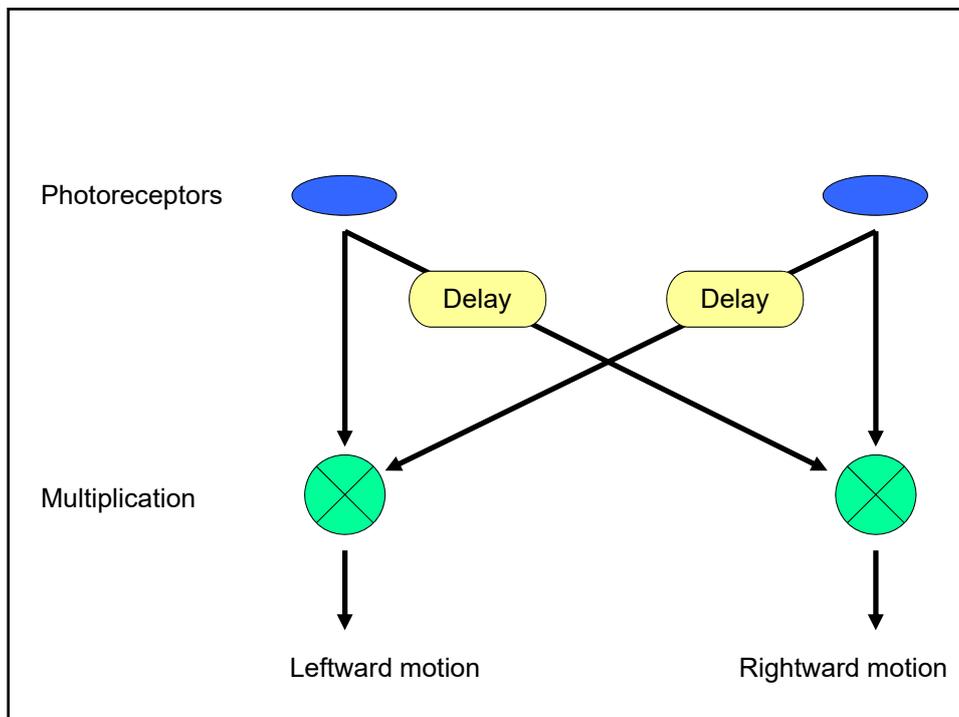
Aliasing

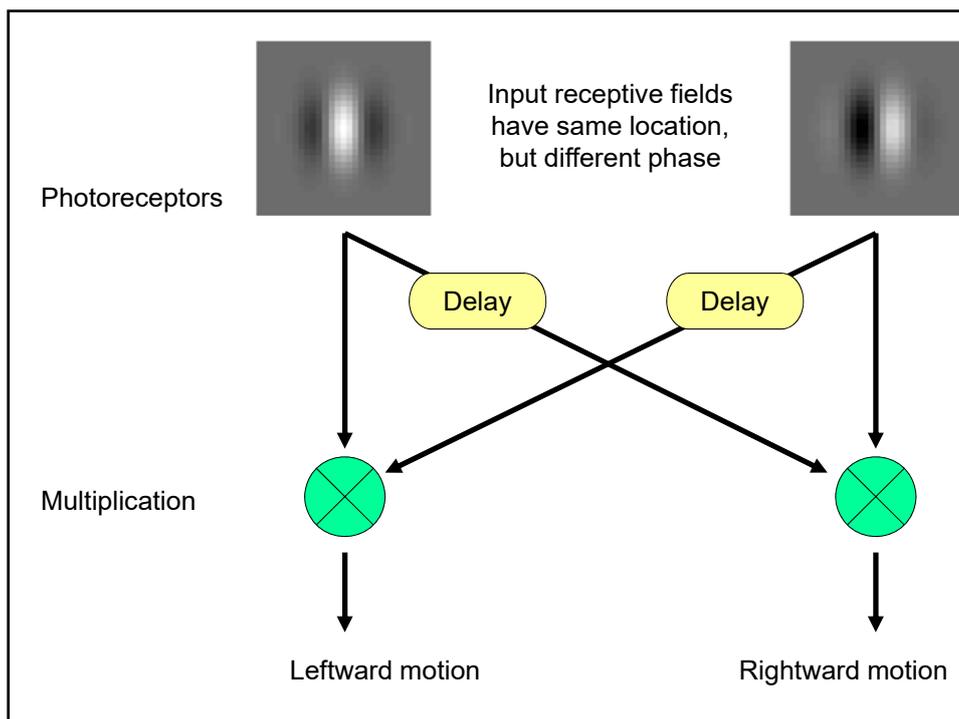
- Happens with movies of periodic patterns when the temporal sampling is too coarse (not enough frames per second)
- With Reichardt motion detector, we can also get aliasing in real-world vision (i.e. not movies) when the delay is too long, or the spatial sampling is too coarse (photoreceptors too far apart)
- This is a good model of motion perception in insects because there is evidence that aliasing occurs in insect vision
- One theory of why zebras have their stripes is that the periodic stripe pattern gives rise to aliasing in the visual systems of biting insects, making them less likely to land on the zebra (How & Zanker, 2014)
- But humans and other mammals show little evidence of aliasing
- van Santen & Sperling (1984) introduced a fix to the Reichardt detector to prevent aliasing
- “Elaborated Reichardt detector”



Aliasing

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Adelson & Bergen (1985)

284 J. Opt. Soc. Am. A/Vol. 2, No. 2/February 1985

E. H. Adelson and J. R. Bergen

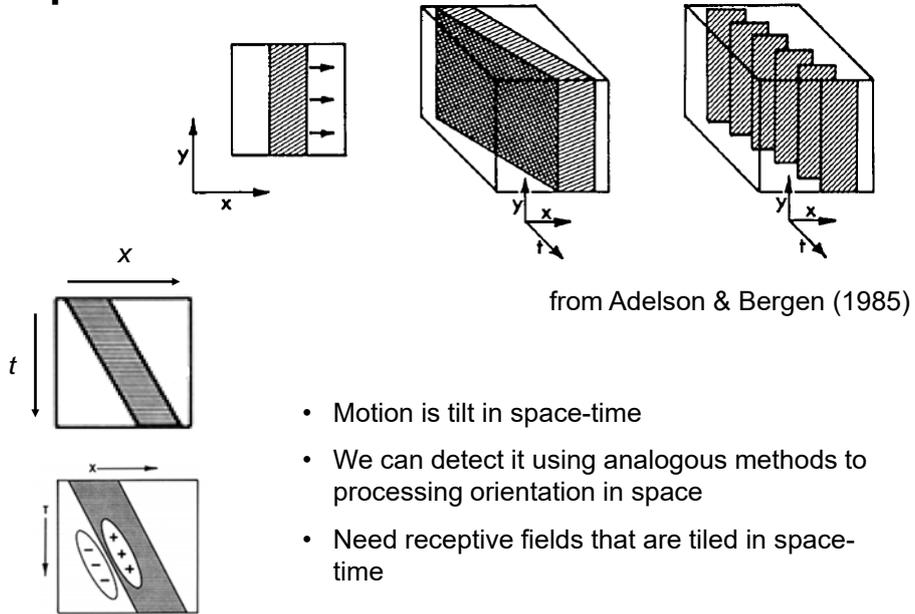
Spatiotemporal energy models for the perception of motion

Edward H. Adelson and James R. Bergen



Edward H. Adelson

Space-time

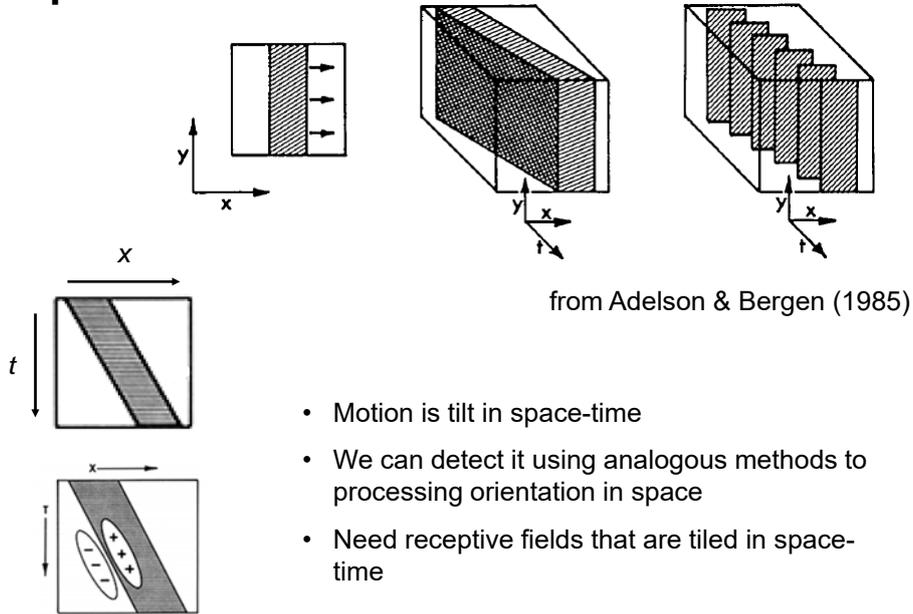


Space-time



Donnie Darko, 2001

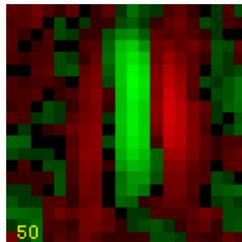
Space-time



- Motion is tilt in space-time
- We can detect it using analogous methods to processing orientation in space
- Need receptive fields that are tiled in space-time

Spatiotemporal receptive fields

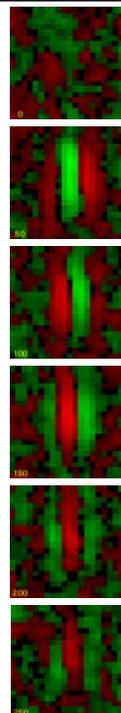
- Spatial receptive field gives the neuron's preferred image



(See DeAngelis, Ohzawa & Freeman, 1993)

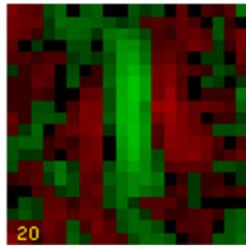
<http://ohzawa-lab.bpe.es.osaka-u.ac.jp/ohzawa-lab/teaching/RF/XTinseparable.html>

- In reality, a neuron has a preferred "movie", the "spatiotemporal receptive field"



Spatiotemporal receptive fields

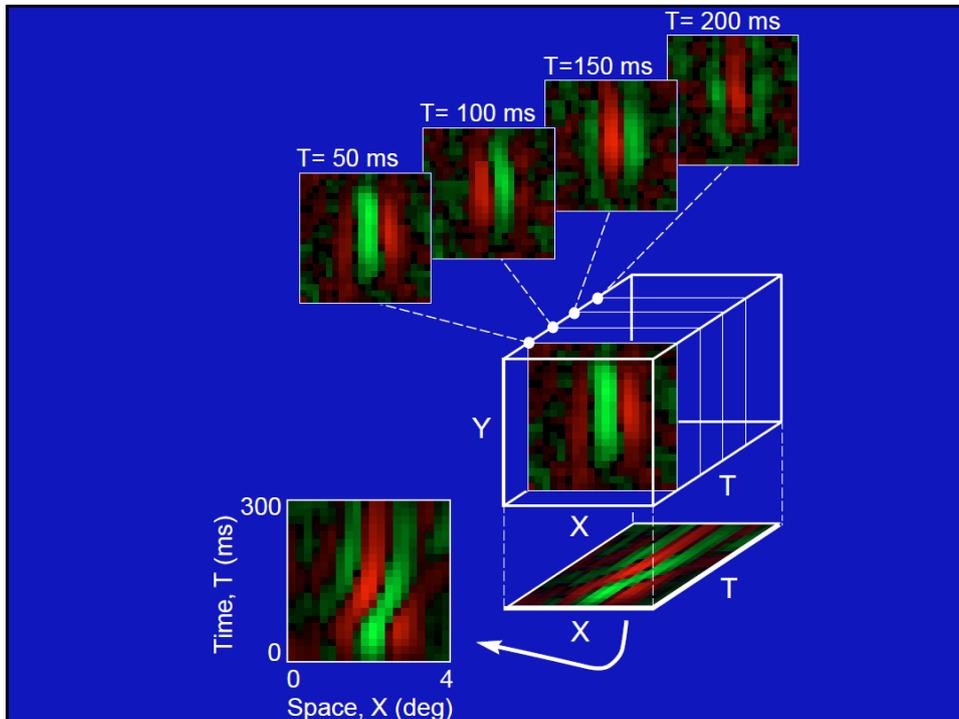
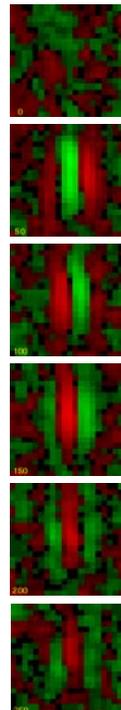
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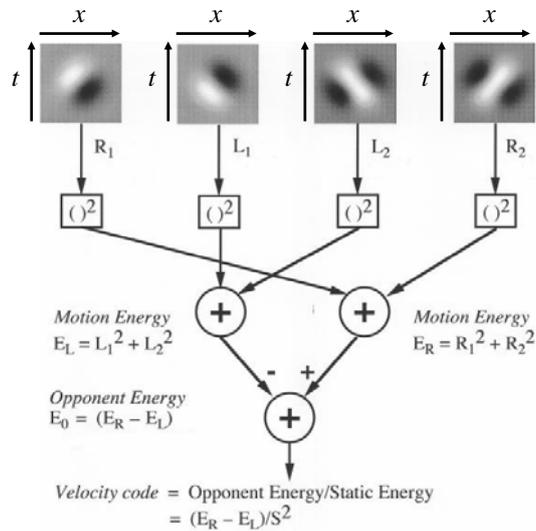
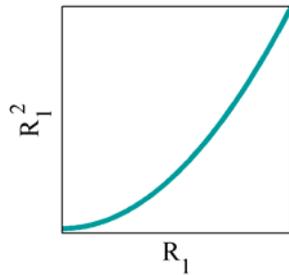
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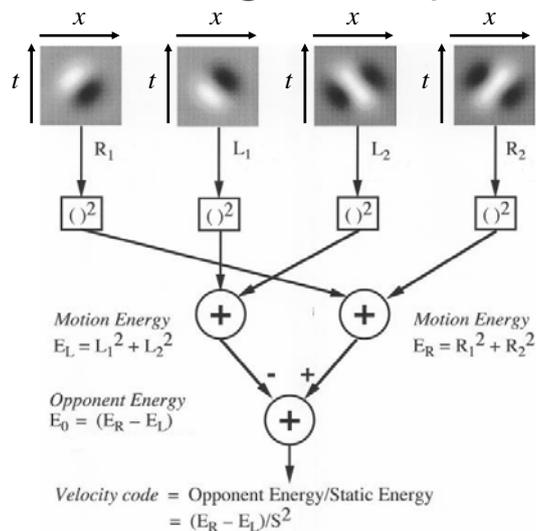
Energy model (Adelson & Bergen, 1985)

- At each point in the image, have simple cells with four types of receptive field
- Put each neuron's output through a squaring function



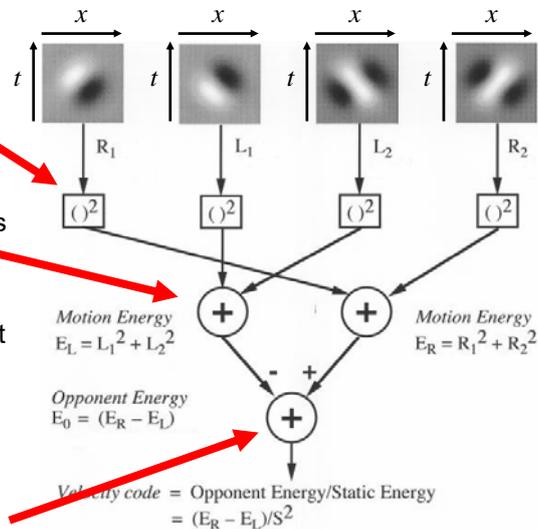
Energy model (Adelson & Bergen, 1985)

- At each point in the image, have simple cells with four types of receptive field
- Put each neuron's output through a squaring function
- Add the squared outputs of the two rightward-selective neurons to give rightward motion energy
- This is a reasonable model of complex cells
- Do the same with the two leftward-selective neurons
- Then subtract leftward from rightward energy to give opponent energy



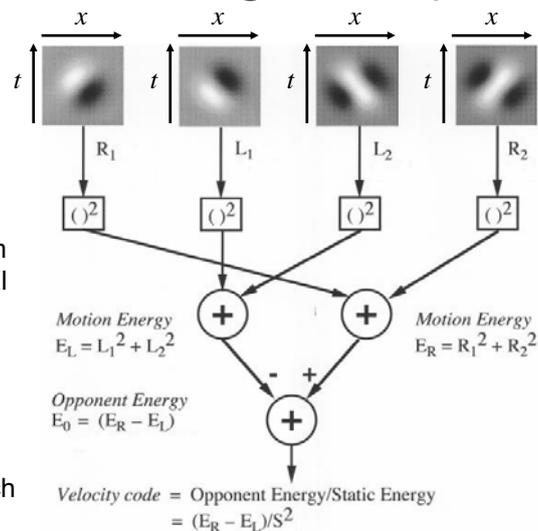
Energy model (Adelson & Bergen, 1985)

- Linear receptive field followed by squaring is a model of simple cells
- Adding outputs of simple cells with odd- and even-symmetric receptive fields is a model of complex cells
- Emerson, Bergen & Adelson (1992) showed that responses of direction-selective complex cells in V1 of cat behaved much like non-opponent motion energy stage
- Qian & Andersen (1994) found evidence for motion opponency in MT



Energy model (Adelson & Bergen, 1985)

- Opponent energy signal increases with signal contrast
- To convert to a pure measure of velocity, divide the opponent energy by a static energy signal, S^2 , from neurons with non-directional receptive fields
- This results in a largely contrast-invariant velocity signal, like MT responses, which are selective for velocity but don't vary much with contrast (Rodman & Albright, 1987; Sclar, Maunsell & Lennie, 1990)

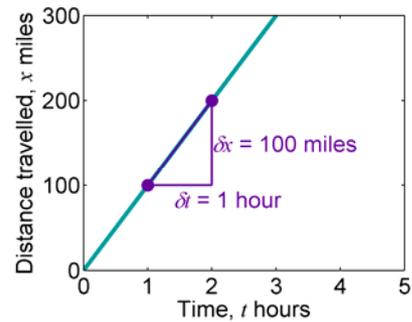


What is motion?

- Change in position over time

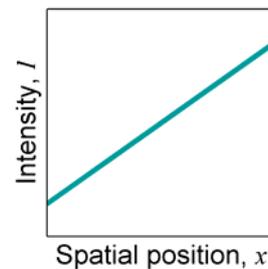
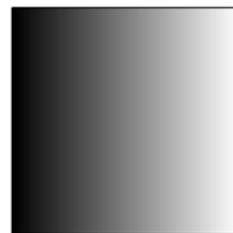
What is speed?

- Rate of change of position
- Distance travelled in a unit of time
- $\frac{\delta x}{\delta t}$ where δx is distance travelled and δt is time taken
- e.g. miles/hour, metres/second
- Speed is the gradient of the plot of distance against time



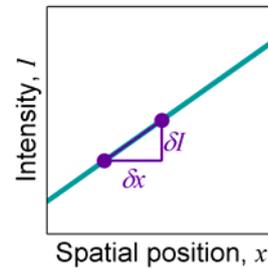
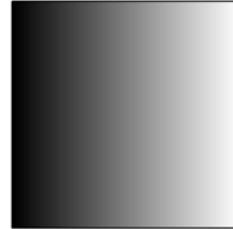
Gradients

- Intensity profile



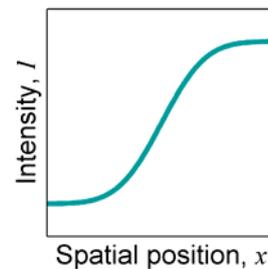
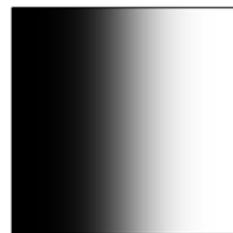
Gradients

- Intensity profile
- Intensity gradient = $\frac{\delta I}{\delta x}$



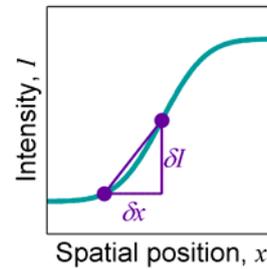
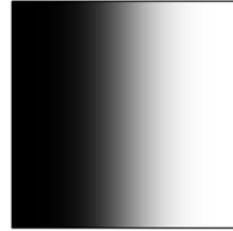
Gradients

- Intensity profile
- Intensity gradient = $\frac{\delta I}{\delta x}$
- With curved profile, gradient is different at each point
- Our previous definition of gradient required two points, so how do we define the gradient *at a point*?



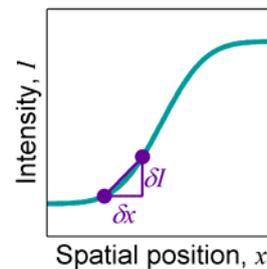
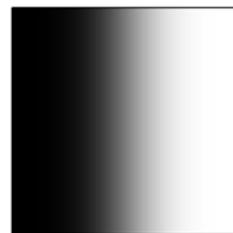
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- Start with two points



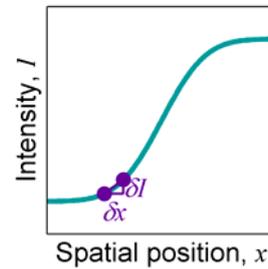
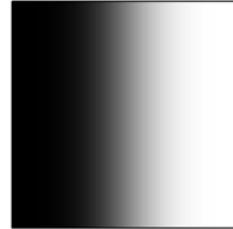
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- Start with two points
- Then gradually make δx smaller



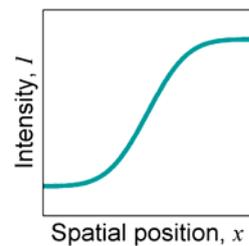
Gradients

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- Our previous definition of gradient required two points, so how do we define the gradient *at a point*?
- Start with two points
- Then gradually make δx smaller
- As δx approaches zero, $\delta I/\delta x$ approaches a limiting value, which we call the *derivative*, written I_x or $\frac{dI}{dx}$
- The derivative is interpreted as the *gradient*, or *rate of change*, at that point



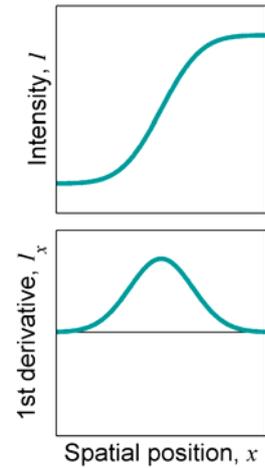
Gradients

- I is the Intensity profile



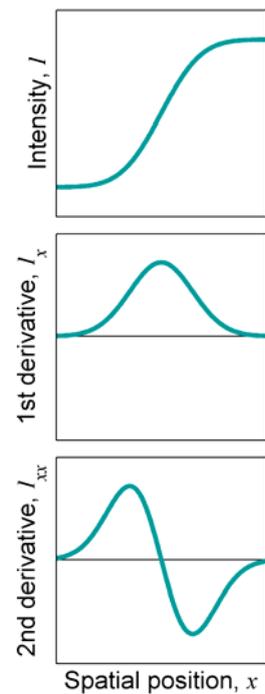
Gradients

- I is the Intensity profile
- I_x is the rate of change of I as we move across space, x



Gradients

- I is the Intensity profile
- I_x is the rate of change of I as we move across space, x
- I_{xx} is the rate of change of I_x as we move across space, x
- I_t is the rate of change of I as we move across time, t
- I_{xt} is the rate of change of I_x as we move across time, t

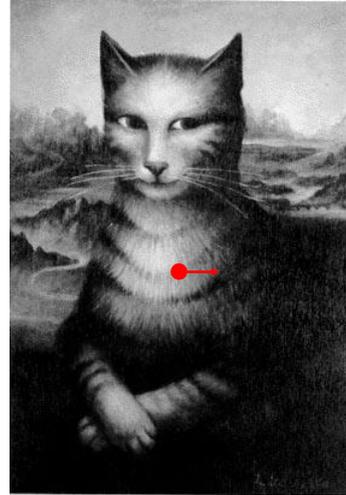


Velocity from intensity gradients

- Move in a positive direction across the image (rightwards)
- Our velocity across the image is $\frac{\delta x}{\delta t}$

$$\frac{\delta x}{\delta t} = \frac{1}{\delta t} \times \frac{\delta x}{1} = \frac{\delta I}{\delta t} \times \frac{\delta x}{\delta I} = \frac{\delta I}{\delta t} \div \frac{\delta I}{\delta x}$$

intensity gradient over time, I_t intensity gradient over space, I_x



- In reality, our analysis mechanisms stay still, and the image content moves
- Moving rightward across image is equivalent to staying still and having image move leftward (negative direction)
- Image velocity is $V = -\frac{\delta x}{\delta t} = -I_t \div I_x$ (Fennema & Thompson, 1979)

Extended gradient model

$$V = -\frac{I_t}{I_x} \quad (\text{Fennema \& Thompson, 1979})$$

- Problem with Fennema & Thompson's algorithm is that velocity estimate gets very large and noise-sensitive when I_x gets close to zero
- We can derive an alternative estimate of velocity based on 2nd derivatives (see Bruce, Green & Georgeson textbook, Box 8.3):

$$V = -\frac{I_{xt}}{I_{xx}}$$

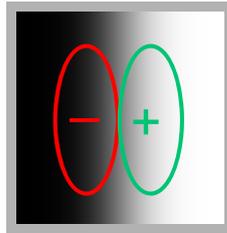
- Johnston, McOwan & Buxton (1992) combined these two velocity estimates (see Bruce, Green & Georgeson textbook, Box 8.3):

$$V = -\frac{I_x I_t + w^2 I_{xx} I_{xt}}{I_x^2 + w^2 I_{xx}^2}$$

- I_x and I_{xx} rarely zero at the same point, so we don't have the problem of division by zero

Measuring spatial intensity gradients

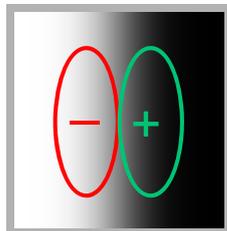
- Spatial intensity gradient is essentially the difference in intensity across a certain distance in the image
- Can be measured using simple cell receptive fields



- Positive gradients cause excitation, i.e. positive response

Measuring spatial intensity gradients

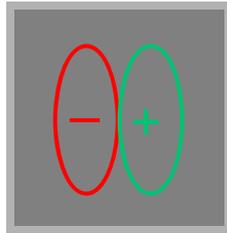
- Spatial intensity gradient is essentially the difference in intensity across a certain distance in the image
- Can be measured using simple cell receptive fields



- Negative gradients cause inhibition, i.e. negative response

Measuring spatial intensity gradients

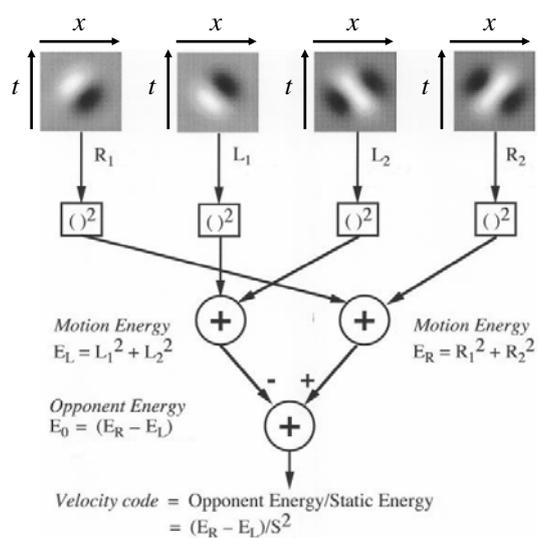
- Spatial intensity gradient is essentially the difference in intensity across a certain distance in the image
- Can be measured using simple cell receptive fields



- Zero gradient gives zero response
- Spatial receptive fields are gradient operators
- Temporal gradients can be measured in a similar way using spatiotemporal receptive fields

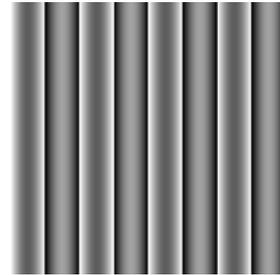
Gradient vs Energy Model

- Gradient model can be implemented with physiologically plausible receptive fields
- Output of the gradient model is mathematically equivalent to the “Velocity code” output of the Energy Model (see Adelson & Bergen, 1986; Bruce, Green & Georgeson textbook, Box 8.4)



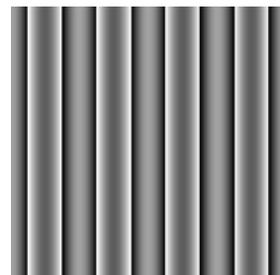
Three equivalent models

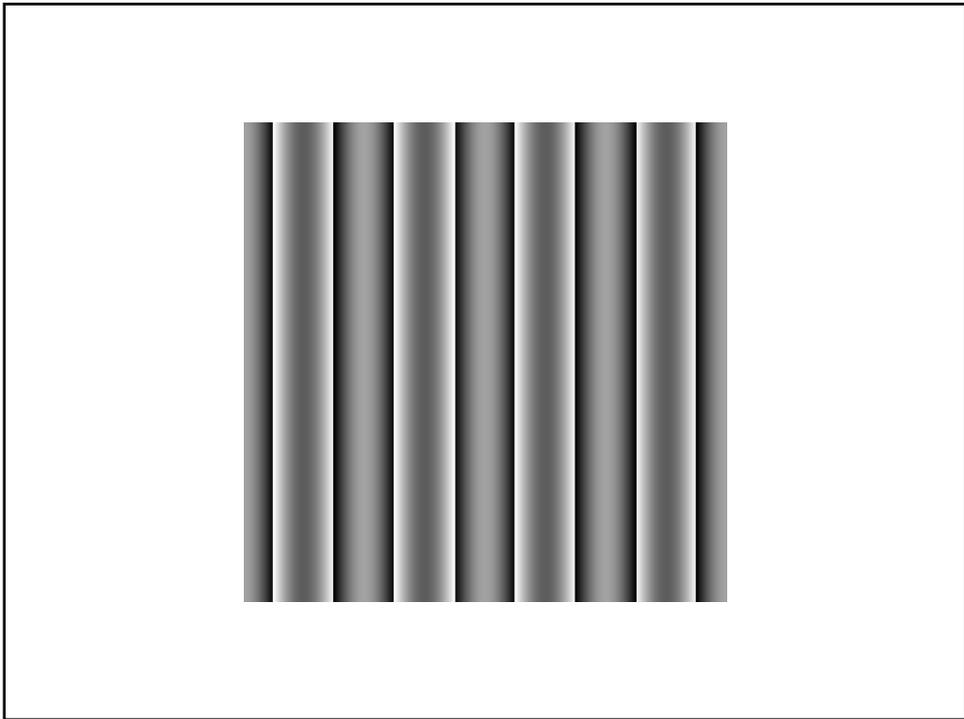
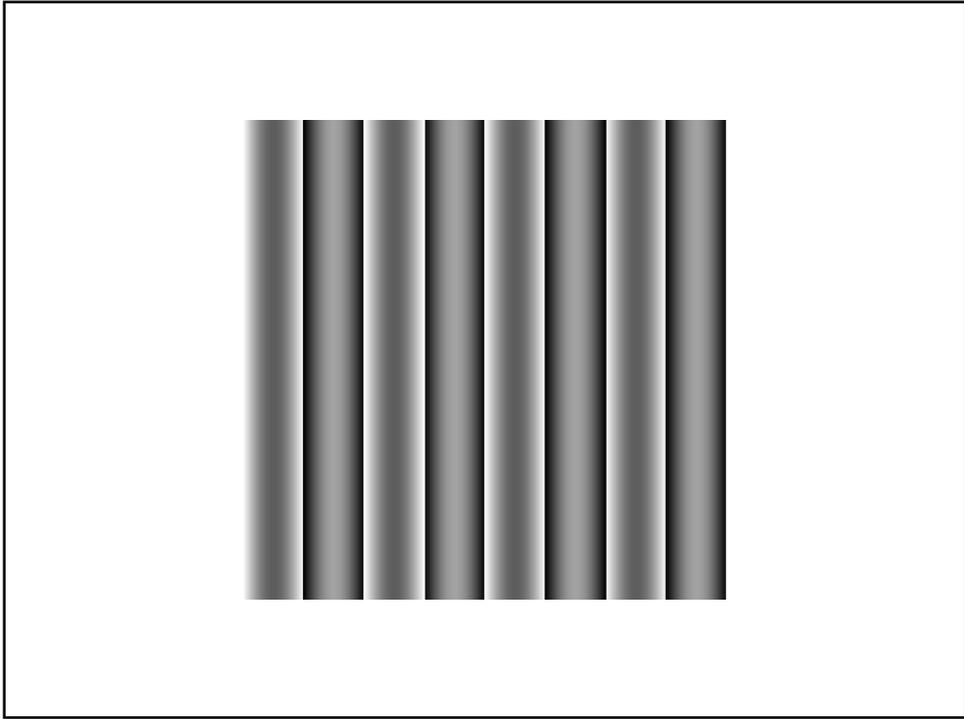
- Energy model gives an insight into the role of the different physiological mechanisms (simple and complex cells in V1, motion opponent cells in MT)
- Gradient model gives a computational insight into why the normalized output of the energy model gives such a good estimate of velocity
- Elaborated Reichardt detector gives a formal link between motion perception in mammals and motion perception in insects
- Energy model correctly predicts perceived direction in the missing fundamental illusion (see Adelson & Bergen, 1985)



Three equivalent models

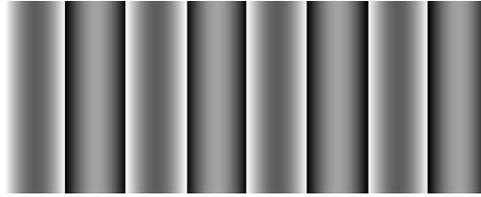
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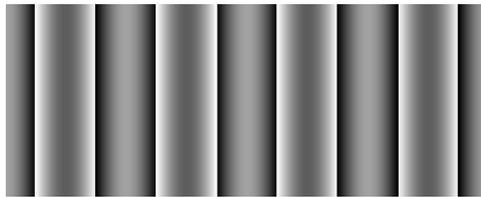


Missing fundamental motion illusion

1st frame

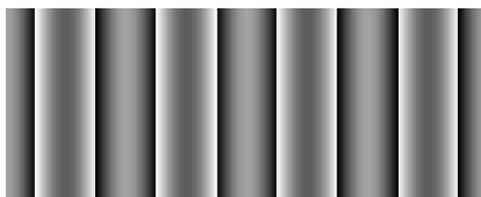


2nd frame

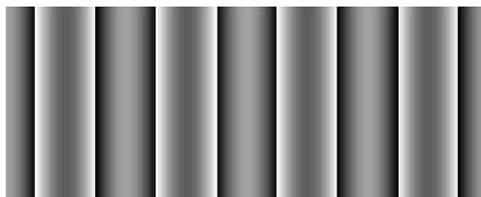


Missing fundamental motion illusion

1st frame



2nd frame

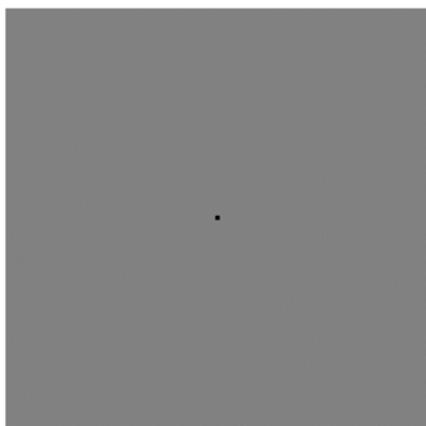


Adelson & Bergen (1985)

Three equivalent models

- Energy model gives an insight into the role of the different physiological mechanisms (simple and complex cells in V1, motion opponent cells in MT)
- Gradient model gives a computational insight into why the normalized output of the energy model gives such a good estimate of velocity
- Elaborated Reichardt detector gives a formal link between motion perception in mammals and motion perception in insects
- Energy model correctly predicts perceived direction in the missing fundamental illusion (see Adelson & Bergen, 1985)
- Gradient model also predicts motion from “motionless” stimuli (e.g. Anstis, 1990)

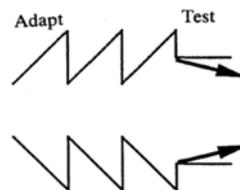
Three equivalent models



illusory
intensity gradient over time, I_t

$$\frac{\delta x}{\delta t} = \frac{\delta I}{\delta t} \div \frac{\delta I}{\delta x}$$

intensity gradient over space, I_x



- Gradient model also predicts motion from “motionless” stimuli (e.g. Anstis, 1990)

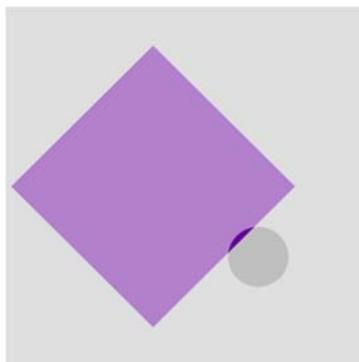
Aperture problem

- Each neuron is effectively looking at the world through a small hole or aperture (its receptive field)
- If you look at the world through a small hole, you are likely to misperceive the motion of objects in the world



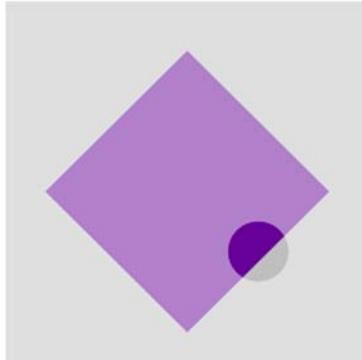
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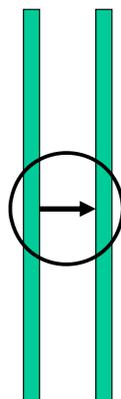


Aperture problem

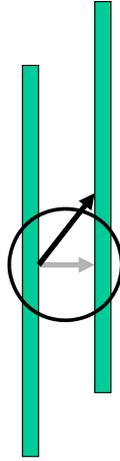
- Each neuron is effectively looking at the world through a small hole or aperture (its receptive field)
- If you look at the world through a small hole, you are likely to misperceive the motion of objects in the world
- Need to integrate motion signals from different parts of the image



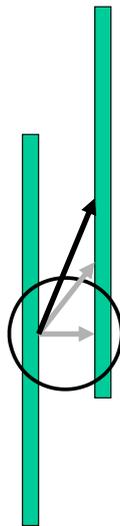
Aperture problem



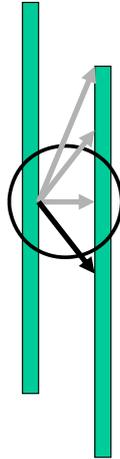
Aperture problem



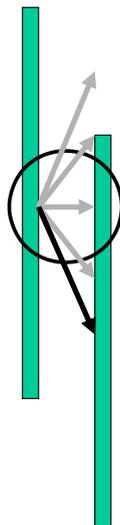
Aperture problem

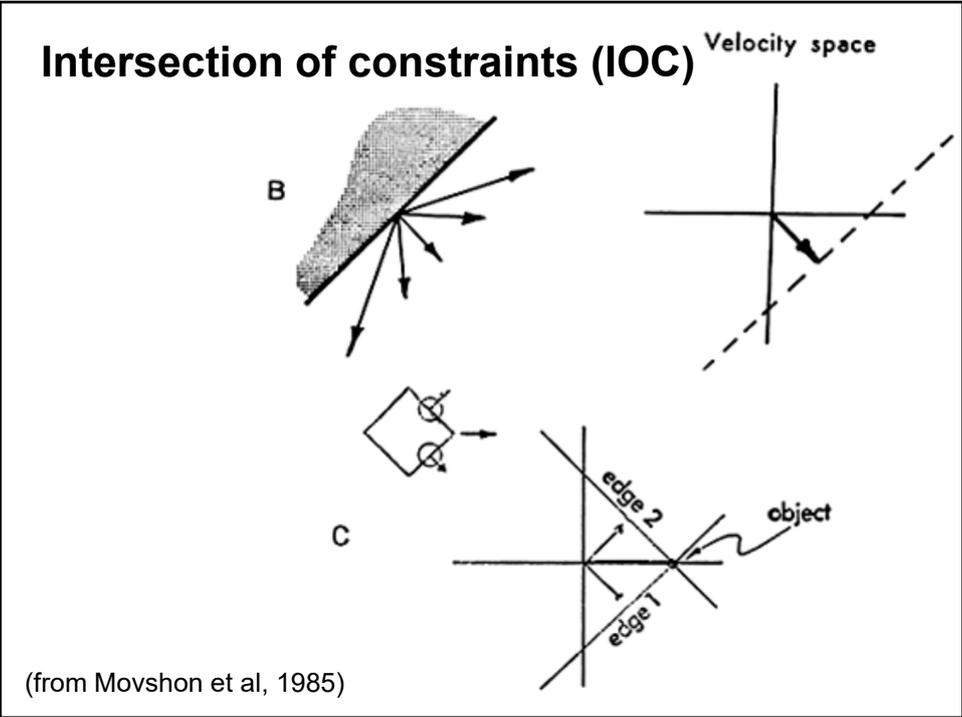
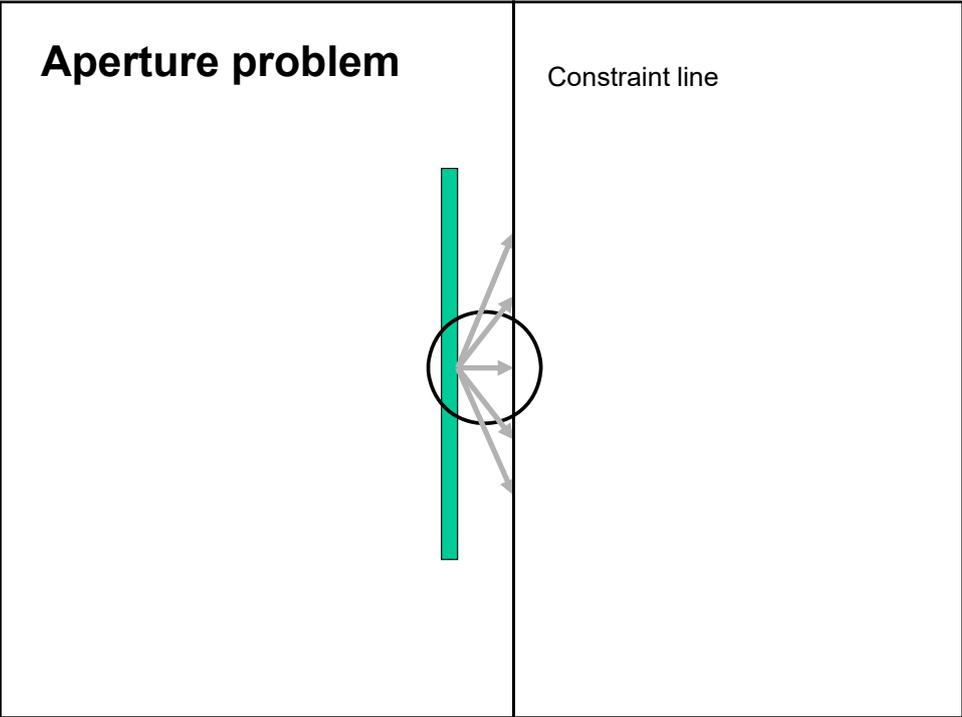


Aperture problem



Aperture problem

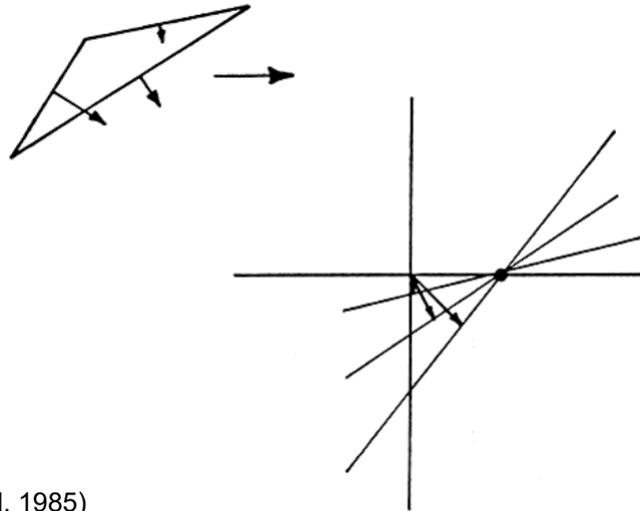




(from Movshon et al, 1985)

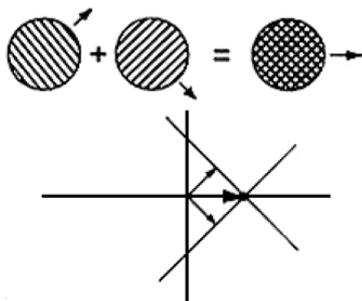
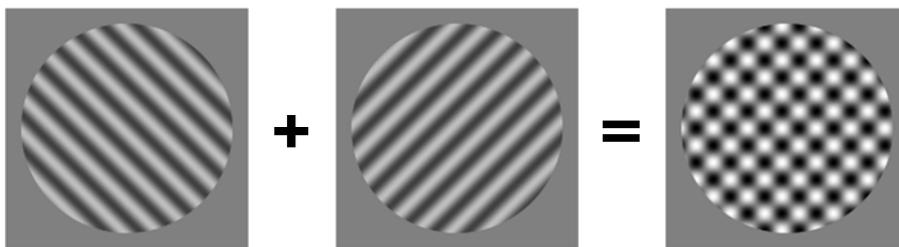
Can we solve IOC by vector averaging?

No!



(from Movshon et al, 1985)

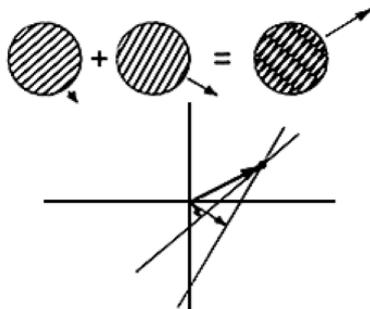
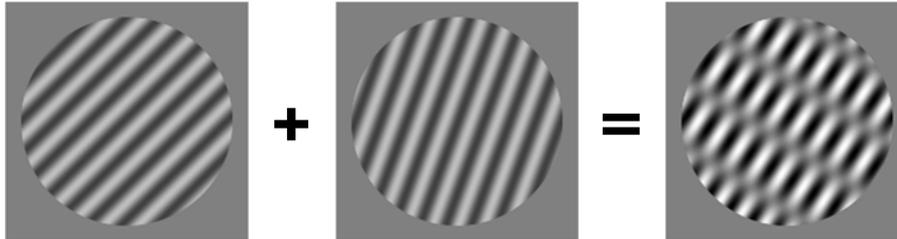
Moving plaid (Adelson & Movshon, 1982)



Type I plaid

- Vector corresponding to the IOC lies between the motion vectors of the individual components, close or equal to the vector average

Moving plaid (Adelson & Movshon, 1982)



Type II plaid

- Motion vectors from individual components both fall on the same side of the IOC vector, so vector average is very different from IOC vector

Coherence (Adelson & Movshon, 1982)

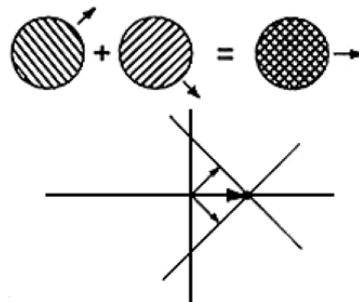
- Plaid components can perceptually cohere or appear as two transparent patterns sliding over each other
- Probability of coherence decreases with
 - decreasing stimulus contrast
 - increasing component speed
 - increasing angle between component directions
 - increasing difference between component spatial frequencies

IOC or vector averaging?

- Ferrera & Wilson (1990) showed that, for Type II plaids, perceived direction was not exactly in the IOC direction – slightly biased towards vector sum direction
- Yo & Wilson (1992) showed that the bias towards vector sum direction increased with
 - decreasing stimulus duration
 - decreasing stimulus contrast
 - increasing eccentricity of viewing
- Wilson, Ferrera & Yo (1992) devised a model which doesn't solve the IOC problem – it integrates the signals in such a way that it often appears to be doing intersection of constraints, but in other situations does not
- Bowns & Alais (2006) have argued that both vector averaging and IOC mechanisms exist in the visual system, and that these multiple solutions “compete to determine perceived motion direction” (p. 1170)

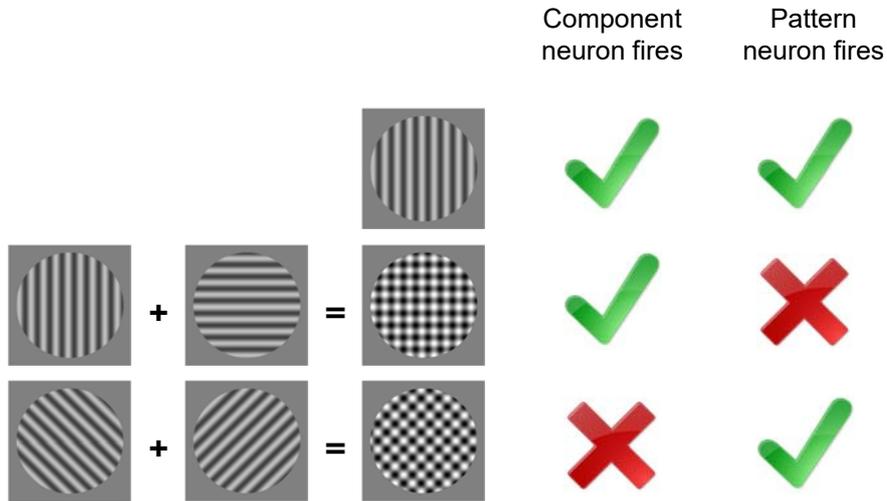
Component vs pattern motion mechanisms

- Key advantage of moving plaids is that the plaid's Fourier components generally move in very different directions from the coherent pattern formed from the combination of the two components
- This allows us to distinguish between mechanisms sensitive to motion of the low-level Fourier components and those sensitive to higher-level pattern motion
- Movshon, Adelson, Gizzi & Newsome (1985) recorded physiological responses to plaids and found
 - V1 neurons were selective for low-level component motion
 - Some MT neurons were selective for low-level component motion
 - Other MT neurons were selective for high-level pattern motion

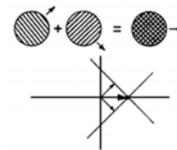
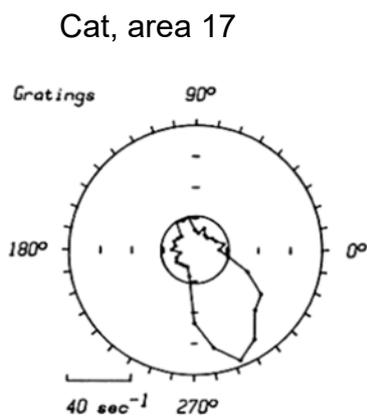


Component vs pattern motion mechanisms

- Suppose we have a neuron selective for rightward component motion, and another selective for rightward pattern motion

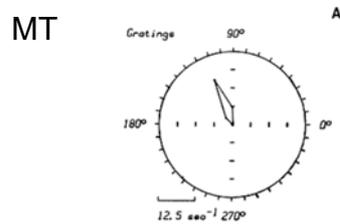


Component vs pattern motion mechanisms



Movshon, Adelson, Gizzi & Newsome (1985)

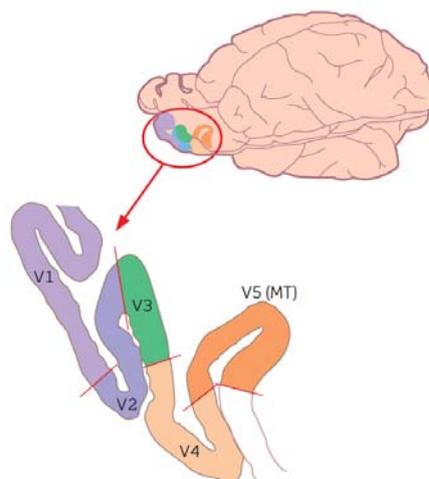
Component vs pattern motion mechanisms



Movshon, Adelson, Gizzi & Newsome (1985)

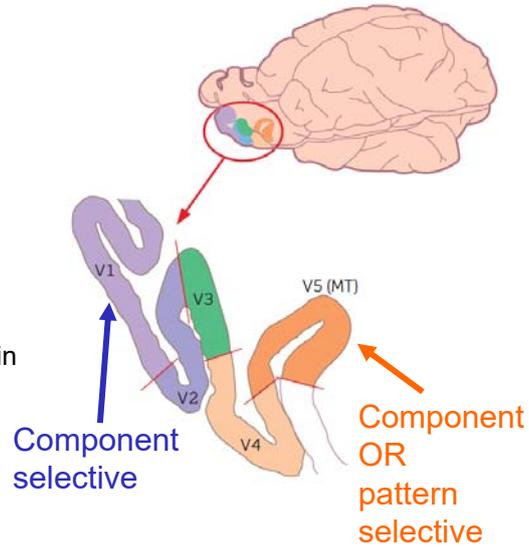
Middle Temporal Area (MT) (also called V5)

- Discovered simultaneously by Dubner & Zeki (1971) and Allman & Kaas (1971)
- Allman & Kaas named it MT because it was in the middle of the temporal lobe of the owl monkey
- Zeki was working on macaques, and named it V5
- MT is nowhere near the middle of the temporal lobe in macaques or humans, but the name stuck
- Main input to MT is from V1

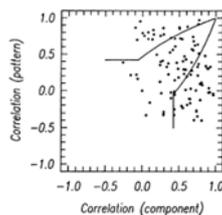
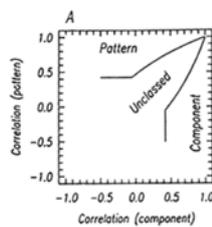


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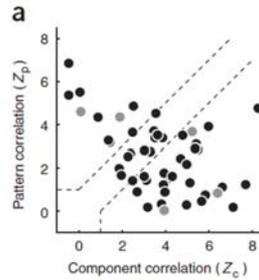


Component vs pattern motion mechanisms



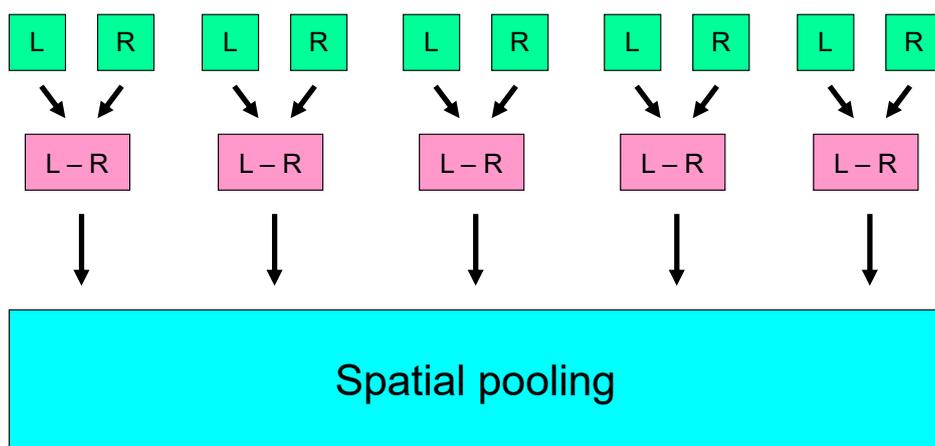
Movshon, Adelson, Gizzi & Newsome (1985)

Component vs pattern motion mechanisms



Rust, Mante, Simoncelli & Movshon (2006)

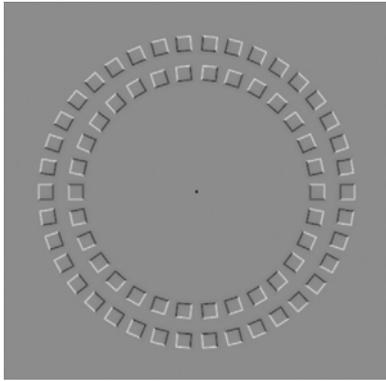
Spatial integration of motion signals in MT



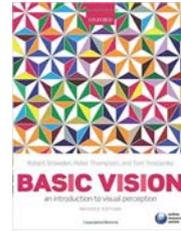
- Each MT neuron pools responses from local motion detectors over a wide area, so it has a large receptive field
- Movshon, Adelson, Gizzi & Newsome (1985)

When spatial integration goes wrong (1)

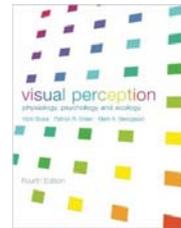
Pinna-Brelstaff illusion



Original version
(Pinna & Brelstaff, 2000)

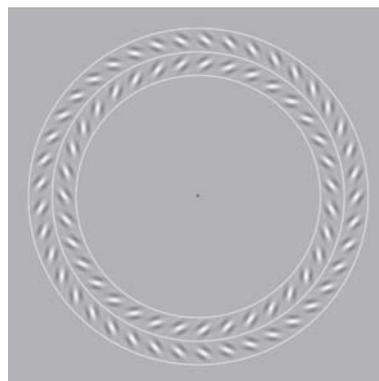


Snowden, Thompson & Troscianko



Bruce, Green & Georgeson

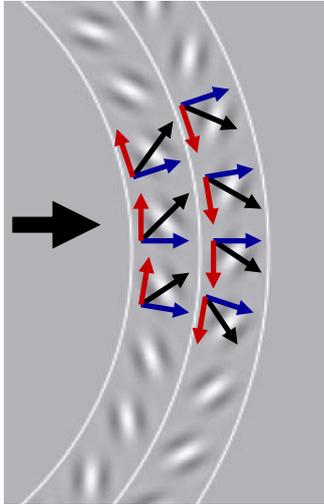
Pinna-Brelstaff illusion



"Optimized" version
(Gurnsey et al., 2002)

When spatial integration goes wrong (1)

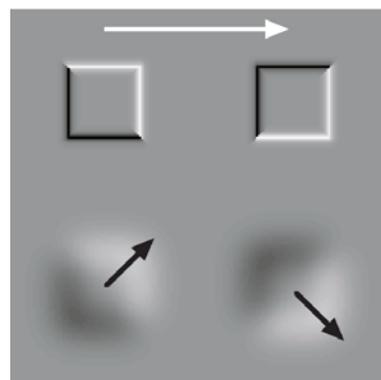
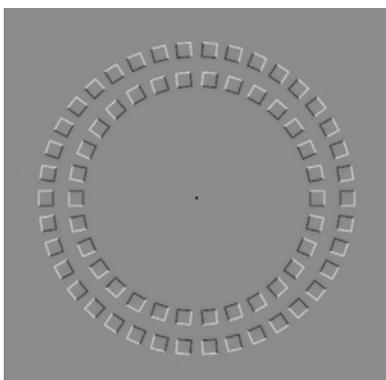
Pinna-Brelstaff illusion



- Local motion detector suffers aperture problem; sees motion towards top right
- Component of motion away from centre interpreted as being caused by looming, so ignored
- That leaves upward motion component
- This is integrated with similar components from the other elements
- Results in illusory motion signal
- Similar thing happens with outer ring
- If motion cues for inner and outer rings were integrated, the illusion wouldn't occur
- Configural cues perceptually segregate inner and outer rings

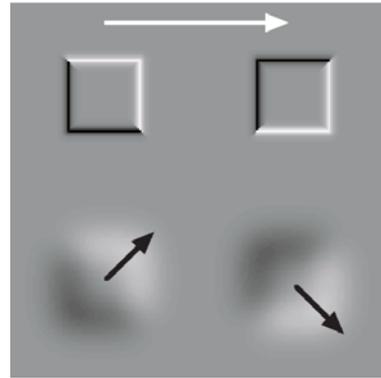
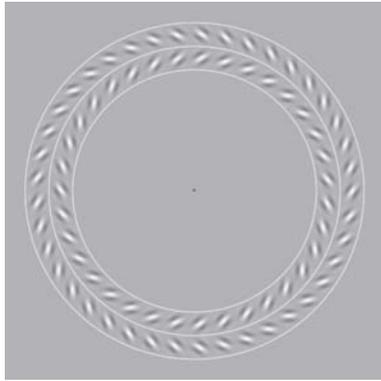
When spatial integration goes wrong (1)

Pinna-Brelstaff illusion



When spatial integration goes wrong (1)

Pinna-Brelstaff illusion



When spatial integration goes wrong (2)

The barberpole illusion



- “Real” motion is leftwards
- Local motion is diagonal, towards top left
- Perceived motion is upwards
- Visual system uses motion of the terminators at the ends of the red-white and blue-white edges to disambiguate motion
- There are more of these along the length of the tube, so their motion dominates perception

When spatial integration goes wrong (2)

The barberpole illusion



- Five different shaped windows onto the same moving grating pattern

When spatial integration goes wrong (2)

The barberpole illusion



- Five different shaped windows onto the same moving grating pattern

When spatial integration goes wrong (2)

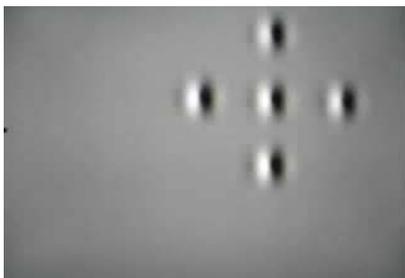
The barberpole illusion



- Five different shaped windows onto the same moving grating pattern

When spatial integration goes wrong (3)

Infinite regress illusion

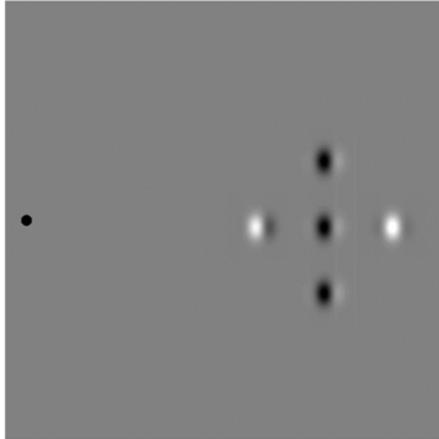


Tse & Hsieh (2006)

<http://illusionoftheyear.com/2006/05/infinite-regress-illusion/>

When spatial integration goes wrong (3)

Infinite regress illusion

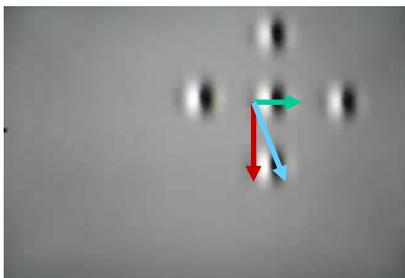


Tse & Hsieh (2006)

<http://illusionoftheyear.com/2006/05/infinite-regress-illusion/>

When spatial integration goes wrong (3)

Infinite regress illusion



- Local motion within each element is rightwards
- Global pattern motion is up and down
- Visual mechanisms in periphery combine these two signals to give diagonal motion

Tse & Hsieh (2006)

<http://illusionoftheyear.com/2006/05/infinite-regress-illusion/>

When spatial integration goes wrong (4)

Curveball illusion (Shapiro Lu Huang Knight & Ennis, 2010)

<http://illusionoftheyear.com/2009/05/the-break-of-the-curveball/>



- In baseball, the pitcher applies spin to the ball
- This causes it to move in a smooth curve
- But the batter also perceives a sudden change of direction, called the “break”
- The break is an illusion

When spatial integration goes wrong (4)

Curveball illusion (Shapiro Lu Huang Knight & Ennis, 2010)

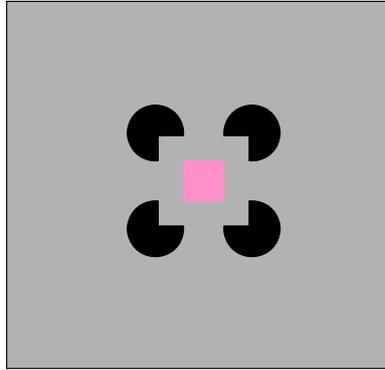
<http://illusionoftheyear.com/2009/05/the-break-of-the-curveball/>



- In baseball, the pitcher applies spin to the ball
- This causes it to move in a smooth curve
- But the batter also perceives a sudden change of direction, called the “break”
- The break is an illusion
- The batter starts off viewing the ball with central vision
- When the ball is close to the batter it may move into peripheral vision
- At that moment, the motion of the seam of the spinning ball starts to be interpreted as object motion, and a sudden change of direction is perceived

When spatial integration goes wrong (5)

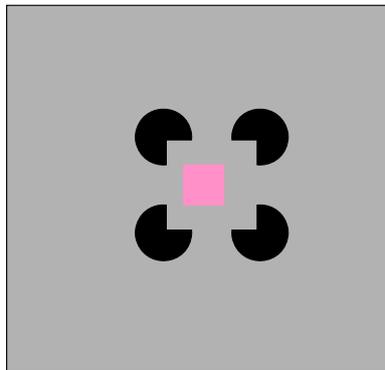
Motion capture (Ramachandran, 1987)



- If the pink square is exactly the same luminance as the background, it will appear to move with the pacman corners

When spatial integration goes wrong (5)

Motion capture (Ramachandran, 1987)



- If the pink square is exactly the same luminance as the background, it will appear to move with the pacman corners

When spatial integration goes wrong (6)

Motion induction (Duncker, 1938)

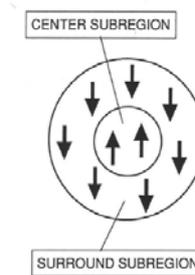
- A stationary object surrounded by motion can appear to move in the opposite direction to the motion (i.e. opposite of motion capture)
- Put a sticker in the middle of the TV screen and watch a football match
- As the camera pans, the sticker appears to move in the opposite direction to the surrounding motion

Reconciling motion induction and capture

- Motion induction causes a stationary object to appear to move in the opposite direction to the surround
- Motion capture causes a stationary object to appear to move in the same direction as the surround
- Murukami & Shimojo (1993) present a model that accommodates both findings
- They show that motion capture happens best with small stimuli or in the periphery
- And motion induction happens best with large stimuli or in central vision

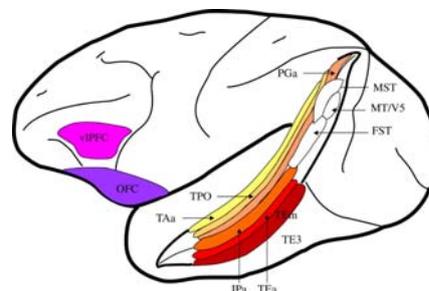
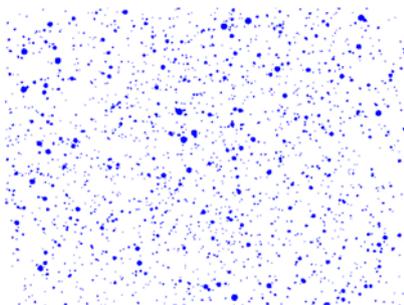
Murukami & Shimojo (1993)

- Their model has MT-like units that pool direction signals over a wide area
- Centre and surround of pooling region tuned to opposite directions of motion
- Unit centred on target is stimulated by, e.g., target moving up or surround moving down
- Surround moving down has same effect on the neuron as target moving up
- Thus, surround moving down is misperceived as target moving up (*MOTION INDUCTION*)
- For small stimuli (or stimuli in the periphery, where receptive fields are large), whole stimulus fits into centre, and motion of surround is pooled with stationary target, and target appears to move in same direction as surround (*MOTION CAPTURE*)
- Neurons with surround tuned to opposite motion direction to centre have been found to MT (Born & Tootell, 1992)



Spatial integration after MT: MST

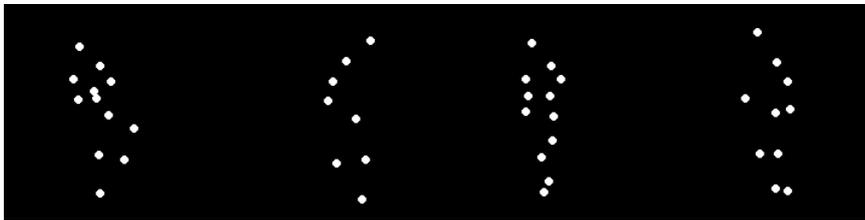
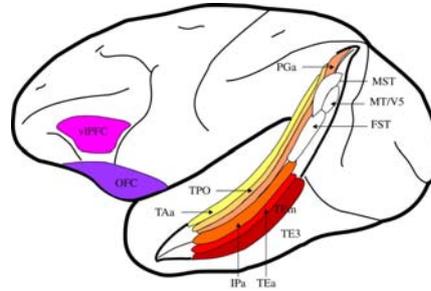
- Area MST contains neurons selective for complex motions such as expansion, rotation, and spiral motion (Duffy & Wurtz, 1991; Tanaka & Saito, 1989)



- These selectivities are not found in MT
- Provide information about self-motion through the environment

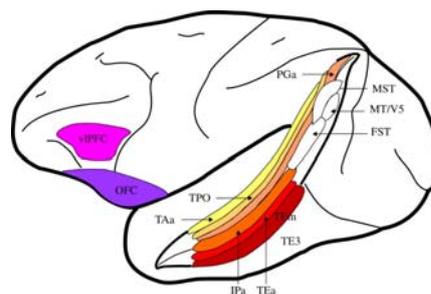
Spatial integration after MT: TPO

- Neurons selective for biological motion found in anterior part of superior temporal sulcus, particularly area TPO (Oram & Perrett, 1994)



Spatial integration after MT: TPO

- Neurons selective for biological motion found in anterior part of superior temporal sulcus, particularly area TPO (Oram & Perrett, 1994)



Discounting eye movements

- Eye movements generate retinal motion signals, but the world doesn't appear to move when we move our eyes
- The visual system must subtract the eye motion from the retinal motion
- How does the visual system know the eye motion?



Outflow theory: use a copy of the motor command signal (Helmholtz, 1866)



Inflow theory: Sense the eye movement directly (Sherrington, 1906)

Testing between inflow and outflow theories



Outflow theory: use a copy of the motor command signal to cancel retinal motion



Inflow theory: Sense the eye movement directly to cancel retinal motion

- If you tap your eye, you cause retinal motion, with no motor command signal
- Outflow theory predicts the world will appear to move
- Inflow theory predicts the world will appear to stay still
- Result of experiment: tapping your eye causes perceived motion

Testing between inflow and outflow theories

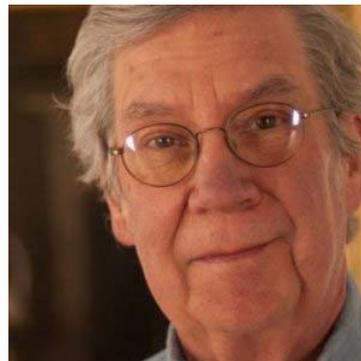
Outflow theory: use a copy of the motor command signal to cancel retinal motion

Inflow theory: Sense the eye movement directly to cancel retinal motion

- Immobilise eye, and try to move it
- Outflow theory predicts the world will appear to move
- Inflow theory predicts the world will appear to stay still
- Result of experiment: Snowden, Thompson & Troscianko say that motion is perceived (*Basic Vision*, p. 176)
- Ernst Mach (1914) immobilised his eyes with putty and claimed to see motion when he tried to move his eyes
- William James (1891) tried it and didn't see motion
- Immobilise eye with drugs that induce muscle paralysis

Stevens et al. (1976)

- John Stevens underwent whole-body paralysis
- After attempted eye movements, he perceived spatial relocation of the visual world *without the perception of motion*
- So, across all the experiments, neither inflow nor outflow theory fully supported



Summary

- Motion aftereffect is evidence of directionally selective opponent processing
- Due to the aperture problem, object motion perception requires motion signals to be integrated over a wide area



- Global pattern motion integrated in MT, and further integration occurs in MST and TPO
- Sometimes the visual system integrates the motion signals in inappropriate ways, leading to illusions of motion

Summary – low-level local motion

- Three key models of low-level local motion perception
 - Motion Energy (Adelson & Bergen, 1985)
 - Gradient model (Johnston, McOwan & Buxton, 1992)
 - Elaborated Reichardt detector (van Santen & Sperling, 1984)
- The outputs of these models can be mathematically equivalent
- But they get the output in different ways
- Motion Energy model gives insight into roles of simple and complex cells in V1
- Gradient model derives a mathematically correct estimate of velocity
- Since Gradient and Energy models can be equivalent, this explains why the energy model's output is such a good estimate of velocity
- These models account for motion illusions such as the missing fundamental illusion

Summary – Global motion

- Aperture problem is solved by integrating motion vectors from multiple components of the image
- Integration appears to proceed via both intersection of constraints and vector averaging
- The different solutions dominate in different situations
- The plaid is a very useful stimulus to investigate global pattern motion
 - Type II plaids make very different predictions for intersection of constraint and vector averaging models
 - The plaid's Fourier components generally move in very different directions from the coherent pattern formed from the combination of the two components
 - This allows us to distinguish between mechanisms sensitive to motion of the low-level Fourier components and those sensitive to higher-level pattern motion
 - V1 neurons are sensitive to component motion
 - Some MT neurons are sensitive to global pattern motion

Further reading

- Chapter 6 of *Basic Vision* (Snowden, Thompson & Troscianko) – simple, entertaining introduction
- Snowden, R.J. & Freeman, T.C.A. (2004). The visual perception of motion. *Current Biology*, 14, R828–R831. **Warning: they get “inflow” and “outflow” theory the wrong way round throughout the paper!**
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- Chapter 8 of *Visual Perception* (Bruce, Green & Georgeson)
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