Neural basis of human visual motion perception

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Neural basis of motion perception

Sensory
How does the brain represent sensory stimuli?

Cognitive
How is this sensory evidence accumulated, remembered, and combined with other information to guide behavior?
Goals

1) *Motion aftereffect*
   - Neural basis of a direction-selective visual illusion

2) *Direction selectivity*
   - Neurons sensitive to direction in human visual cortex

3) *Direction of moving objects*
   - Neurons that represent direction of object motion
fMRI

**BOLD signal**
- neural activity $\rightarrow$ oxygen demand $\rightarrow$
  proportion of deoxygenated hemoglobin $\rightarrow$ MRI signal

**Resolution**
- spatially coarse, temporally sluggish

**Average spiking activity**
- space: across each visual cortical area
- time: across several seconds
Human visual cortex
Motion responses in human visual cortex

moving vs stationary

MT+
1

Neural basis of the motion aftereffect
Motion aftereffect

Addams, 1834
Motion aftereffect

MAE adapt blank test blank

25.5 sec 18 sec 5 sec 19 sec
Motion aftereffect

25.5 sec  18 sec  5 sec  19 sec
Motion aftereffect

- Adapt: 25.5 sec
- Blank: 18 sec
- Test: 5 sec
- Blank: 19 sec
Motion aftereffect

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Motion aftereffect

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Motion aftereffect

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fMRI experiment

| control | MAE | MAE | control | control | MAE |
fMRI experiment

MT+ responses on MAE trials
fMRI experiment

| control | MAE | MAE | control | control | MAE |

MT+ responses on MAE trials

Average MAE time series

Adapt  Blank  Test
Motion aftereffect

*Difference in MT+ activity during MAE vs control?*
Motion aftereffect

MAE > control


Direction-selective neurons

Monkey MT, MST: > 90% of neurons are direction-selective
Motion aftereffect: Theory

stimulus

neural response

perceived direction

stationary

L | R

NONE
Motion aftereffect: Theory

stimulus

neural response

perceived direction

stationary

rightward

NONE

RIGHT
Motion aftereffect: Theory

- Stimulus: stationary
- Neural response:
  - L
  - R
- Perceived direction:
  - NONE
  - RIGHT

Adaptation
Motion aftereffect: Theory

stimulus
neural response
perceived direction

stationary

rightward

adaptation

NONE

RIGHT
Motion aftereffect: Theory

- **stimulus**: stationary
- **neural response**: L R
- **perceived direction**: NONE
- **rightward**: adaptation
Motion aftereffect: Theory

stimulus

neural response

perceived direction

stationary

rightward

stationary

stationary

NONE

RIGHT

LEFT
Motion aftereffect: Theory

Direction-selective reduction in response

Cat Primary Visual Cortex
Giaschi et al 1993
Marlin et al 1988
Saul & Cynader 1989
Vautin & Berkeley 1877
von der Heydt et al 1973

Monkey MT
Petersen et al 1985
van Wezel & Britten, 2001, 2002
Motion aftereffect: Puzzle

fMRI
net increase

theory + single neurons
direction-selective decrease

MAE
illusory motion

control
no motion

attention increases MT+ responses

e.g., Beauchamp et al 1997
Treue & Martinez Trujillo 1999
Huk & Heeger 2000
Equating attention during test period

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25.5 sec 18 sec 5 sec 19 sec

equate attention
Equating attention during test period

**motion task:**
which patch moved outward faster?

- performed on both MAE and control trials
- equal, threshold difficulty

5 sec test
Motion aftereffect

*Difference in MT+ activity during MAE vs control when attention is equal?*
Motion aftereffect with controlled attention

MAE = control

Summary: Motion aftereffect

MT+ responses are affected by attention to MAE

Motion aftereffect does not necessarily depend on a net increase in MT+ response

*Direction-selectivity?*
2

Direction-selectivity in human visual cortex
Direction-selective adaptation

*Direction-selective response decrease*

- Compare Repeated vs Mixed

  (e.g., Grill-Spector et al, 1999; Kourtzi & Kanwisher, 2001)
Direction-selective adaptation

Mixed direction

Adapted direction
Direction-selective adaptation

Mixed direction

Adapted direction
Direction-selective adaptation

Mixed direction

Adapted direction
Direction-selective adaptation

Mixed direction

Adapted direction
Direction-selective adaptation

Control attention speed task

Mixed direction

Adapted direction

... X 12

... X 12
fMRI experiment

mixed direction  adapted direction  mixed direction  adapted direction

0  18  36  54  72

time (sec)

× 6

adaptation response amplitude
Direction-selective adaptation?
Direction-selective adaptation

Huk, Ress, & Heeger, Neuron (2001)
Direction-selectivity in human visual cortex

**direction-selectivity index**
(adaptation response / baseline response)

Summary: Direction-selectivity

Direction-selective neurons, increasing across visual cortex, strongest in MT+

Direction of moving objects?
3
Direction of moving objects
Gratings and plaids

component grating 1

+ component grating 2

= plaid pattern
Component and pattern motion cells

**component-motion cells**
- direction of local components

= grating component moving
→ *strong response*

**pattern-motion cells**
- direction of objects and patterns

≠
Component and pattern motion cells

component-motion cells
direction of local components

\[ \text{pattern moving} \rightarrow \text{strong response} \]

pattern-motion cells
direction of objects and patterns

\[ \text{grating component moving} \rightarrow \text{strong response} \]

Movshon et al, 1986
Albright, 1984
Human cortex

component-motion cells + pattern-motion cells
Selective adaptation protocol

Adapted direction

Mixed direction
Selective adaptation protocol

Adapted direction

Mixed direction
Selective adaptation protocol

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Selective adaptation protocol

Adapted direction

Mixed direction
Selective adaptation protocol

Adapted direction

Mixed direction
Trials

plaid motion

1.3 sec 0.7 sec
Trials

plaid motion

1.3 sec 0.7 sec

response

× 8
fMRI experiment

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<thead>
<tr>
<th>mixed direction</th>
<th>adapted direction</th>
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× 6

time (sec)
Average fMRI response

fMRI response
(% BOLD change)

time (sec)

mean
Predictions: Pattern-motion activity

**fMRI response** (% BOLD signal change)

**Modulation** of pattern-motion response

**Plaid direction**

mixed direction

adapted direction

0 16 32

time (s)
Predictions: Component motion activity

Component direction

fMRI response (% BOLD signal change)

No modulation of component-motion response
Pattern motion adaptation

Modulation of pattern motion response?
Pattern motion adaptation

Pattern motion adaptation

fMRI response (% BOLD signal change)

MT+

no adaptation when plaid direction varies

(p = .35 - .74)

Pattern motion selectivity across visual cortex

Pattern-motion direction-selectivity index
(adaptation response / baseline response)

Pattern motion perception

\[ \text{strong pattern-motion percept} \]
Pattern motion perception

Adelson & Movshon, 1982
Pattern motion perception

Adapted direction

Mixed direction
Pattern motion perception

Adapted direction

Mixed direction
Pattern motion perception

Adapted direction

Mixed direction
**Pattern motion perception**

Pattern motion perception

Pattern motion perception

Equally strong adaptation with high + low SF plaidsin (p = .93)

fMRI response (% BOLD signal change)

MT+

-0.2

0

0.2

0

16

32

time (s)

mixed direction

adapted direction

Pattern motion perception

Relation between fMRI response and percept

Summary: Pattern motion

Pattern-motion selectivity in human visual cortex

Early visual areas represent component motions, later areas (MT+) represent pattern motion

Strength of pattern-motion activity corresponds to strength of pattern-motion percept
Conclusions

**Neural basis of human motion perception**

- **Neurons**: Direction-selectivity in human cortex
- **Processing**: Component-motion $\rightarrow$ pattern-motion
- **Perception**: Relative response strengths correspond to motion percepts
Conclusions

Human / monkey homology

- Strong direction-selectivity, pattern-motion in: human MT+ ⇔ monkey MT/MST
- Human MT+ subdivisible into MT and MST  
  (Huk, Dougherty, & Heeger, *J Neurosci*, 2002)
Passive viewing vs controlled attention

Responses were not saturated during task performance.

Response to moving test stimulus 70% larger ($p \sim 0$)

$\rightarrow$ Responses were not saturated during task performance
Future directions: Decision

Accumulation of evidence

Sensory [MT]  ?  Decision [LIP]
Future directions: Decision

*Combination of sensory evidence and other knowledge*
Future directions: Decision

*Combination of sensory evidence and other knowledge*

Bias $\xrightarrow{?} \text{Decision [LIP]}$
Future directions: Decision

Combination of sensory evidence and other knowledge

Bias \quad ? \quad Decision [LIP]

1) start point: boost baseline?
Future directions: Decision

Combination of sensory evidence and other knowledge

Bias

1) start point: boost baseline?
2) weighting: steepen slope?

Decision [LIP]
Future directions: Decision

Combination of sensory evidence and other knowledge

Bias

? 

Decision [LIP]

1) start point: boost baseline?
2) weighting: steepen slope?
3) threshold: lower maximum?
Collaborators

**fMRI**
David Heeger
David Ress
Bob Dougherty
Geoff Boynton

*Monkey single-units and psychophysics*
Mike Shadlen, John Palmer

*Retinotopy, gray matter segmentation & flattening*
Brian Wandell, Alex Wade, Alyssa Brewer

**MR Physics**
Gary Glover
Future directions: Sensory

**Speed**

**selective adaptation**: separate sensitivity to speed from temporal and spatial frequencies
The aperture problem
The aperture problem
The aperture problem

“**Component motion**” cells
aperture problem

“**Pattern motion**” cells
object motion
Future directions: Decision

Accumulation of evidence
Functional subdivision of human areas MT and MST
Monkey MT / MST complex

**MT**  translation
smaller receptive fields
retinotopic organization

**MST**  optic flow
larger receptive fields
no clear retinotopy
Strategy: MT+ subdivision

<table>
<thead>
<tr>
<th>Localizer [MT+]</th>
<th>Retinotopy [MT]</th>
<th>Ipsilateral [MST]</th>
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<tbody>
<tr>
<td>• all motion responsive neurons</td>
<td>• small receptive fields</td>
<td>• large receptive fields</td>
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<tr>
<td></td>
<td>• retinotopic organization</td>
<td>• no retinotopy</td>
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Localizing MT+
Retinotopy stimulus

Wedge of moving dots

motion-wedge rotates slowly through visual field
Retinotopy and receptive field size

small RF [MT]

no response

... strong response

strong modulation

large RF [MST]

moderate response

... moderate response

weak modulation
Ipsilateral stimulus

Ipsilateral motion

10 deg

Ipsilateral stationary
Ipsilateral stimulus and receptive field size

small RF [MT]

no response

large RF [MST]

ipsilateral response
Strategy: MT+ subdivision

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Subdividing human MT+

Localizer [MT+]
Retinotopy [MT]
Ipsilateral [MST]
Subdividing human MT+

Localizer [MT+]  Retinotopy [MT]  Ipsilaterial [MST]
Summary: Subdivision of MT+

- Human MT+ is subdivisible into MT, MST
- MT contains a retinotopic map of motion direction
- MST neurons summate motion over larger regions of space
Direction-selective adaptation
Direction-selective adaptation

![Diagram showing direction-selective adaptation with an image of a black box on a striped background and a time chart showing the opposite-direction process with adapt, test, and response phases.]
Direction-selective adaptation

Speed task: control attention
Direction-selective adaptation

![Diagram showing direction-selective adaptation](image)

**opposite-direction**

<table>
<thead>
<tr>
<th>adapt</th>
<th>test</th>
<th>response</th>
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<tr>
<td>4 sec</td>
<td>0.5 sec</td>
<td>1 sec</td>
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**adapted-direction**

<table>
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<tr>
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<th>test</th>
<th>response</th>
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Direction-selective adaptation

Speed task: control attention

opposite-direction

adapt

4 sec

test

0.5 sec 1 sec

response

adapted-direction

adapt

response

X 3

X 3
fMRI experiment

<table>
<thead>
<tr>
<th>opposite direction</th>
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The graph shows a sinusoidal pattern with alternating periods of opposite and adapted directions. Each cycle is multiplied by 6, indicating a significant increase in amplitude. The time (sec) is marked at intervals of 16 seconds, from 0 to 54 seconds.

The response is depicted by the graph, showing a gradual increase in amplitude over time, with specific notation for adaptation.
Direction-selective adaptation

Opposite-direction > Adapted-direction

MT+

Direction-selective adaptation

\[ \Downarrow \]

\textit{Direction-selectivity}

Huk, Ress, & Heeger, \textit{Neuron} (2001)
Pattern-motion controls

Weak effects just due to SFs?

strong

weak
Pattern-motion controls

Weak effects just due to SFs?

\[ \begin{align*}
\text{strong} & \quad \text{weak} \\
\end{align*} \]
Pattern-motion controls

*Weak effects just due to SFs?*
→ No. Strong adaptation with coherent high and low-SF plaids. 
\( F_{1,55} = 0.07, p = .93 \)

*Were responses really due to direction-selective adaptation?*
Pattern-motion controls

Weak effects just due to SFs?
→ No. Strong adaptation with coherent high and low-SF plaids.
   \((F_{1,55} = 0.07, p = .93)\)

Were responses really due to direction-selective adaptation?
→ Yes. Rotating plaid direction from trial to trial produced no response modulation.
   \((p = .35 - .74)\)
Conclusions

Adaptation

- Characterize neural response properties
- Quantify selectivity across visual areas
- Selectively isolate hierarchical stages of processing