Cognitive Neuroscience
9/2/21

Motion Processing in the Visual System

1. Organization of cortical visual areas

2. Akinetopsia in humans

3. MT: an area specialized for processing visual motion

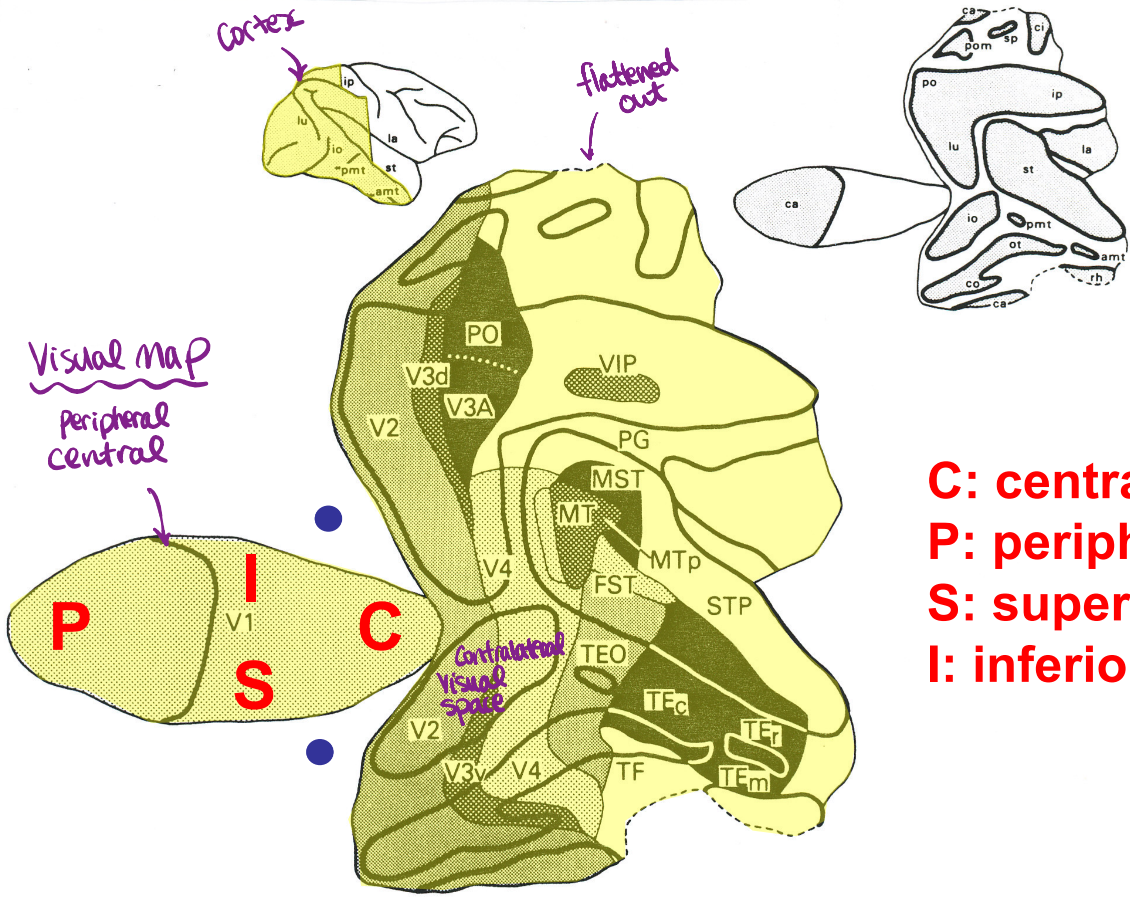
4. Neuronal firing in MT <----> motion perception

5. Functional activation of MT in humans

Desimone & Ungerleider (1989)
Handbook of Neuropsychology, Vol. 2
Elsevier, pp. 267-299

Visual cortex in monkeys and humans consists of numerous contiguous areas spanning the occipital lobe and adjacent parts of the temporal and parietal lobes.

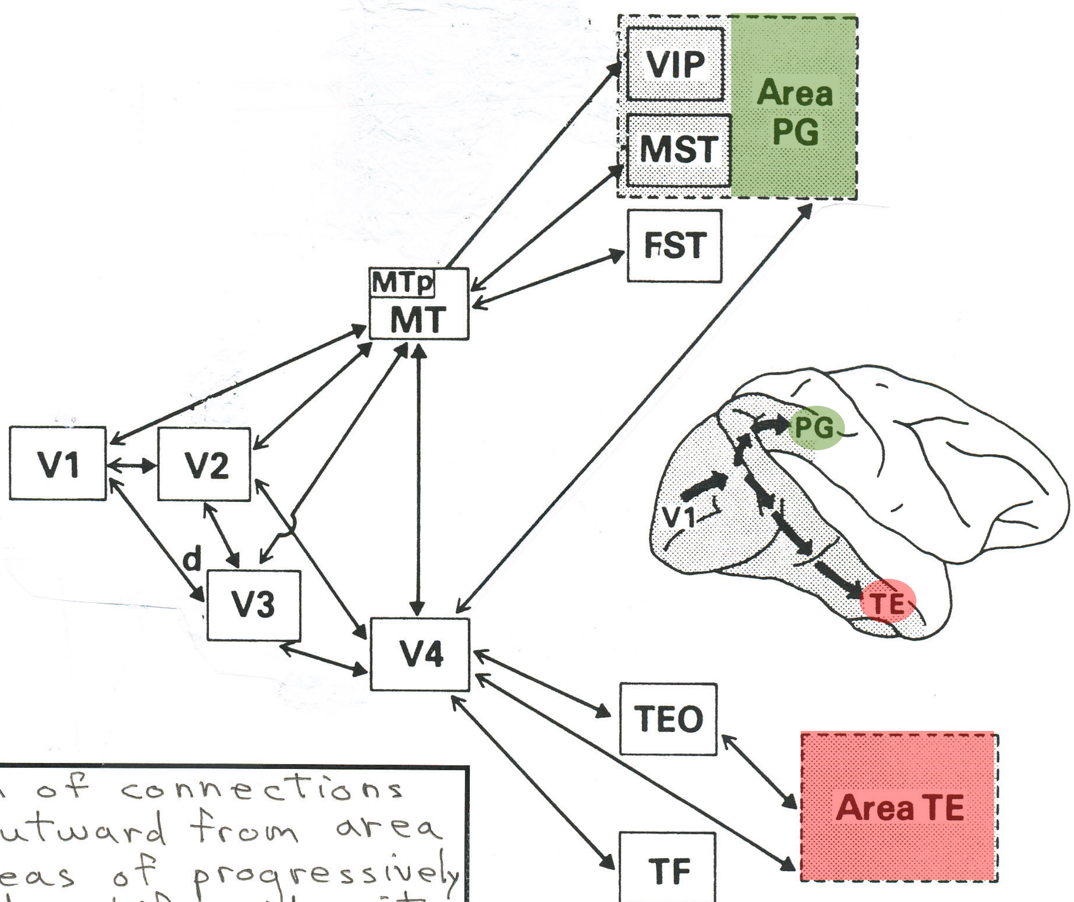
There are a bunch of independent visual areas



C: central
P: peripheral
S: superior
I: inferior

Fig. 2. Cortical visual areas in the macaque, shown on a flattened representation of the cortex. The portion of the cortex flattened is shown in grey on the small lateral view of the hemisphere (upper left). The major sulci are shown in grey on the small flattened map (upper right). It was necessary to 'cut' the map at the border of V1 in order to flatten it (Van Essen and Maunsell, 1980). The large map shows the locations of many of the known visual areas. Areas PG, TF and STP are shown in white without borders, since the boundaries and/or subdivisions of their visual portions are not yet clear. Abbreviations: amt, anterior middle temporal sulcus; ca, calcarine fissure; ci, cingulate sulcus; co, collateral sulcus; io, inferior occipital sulcus; ip, intraparietal sulcus; la, lateral sulcus; lu, lunate sulcus; ot, occipitotemporal sulcus; po, parieto-occipital sulcus; pmt, posterior middle temporal sulcus; pom, medial parieto-occipital sulcus; rh, rhinal fissure; sp, subparietal sulcus; st, superior temporal sulcus. Figure adapted from Ungerleider and Desimone (1986).

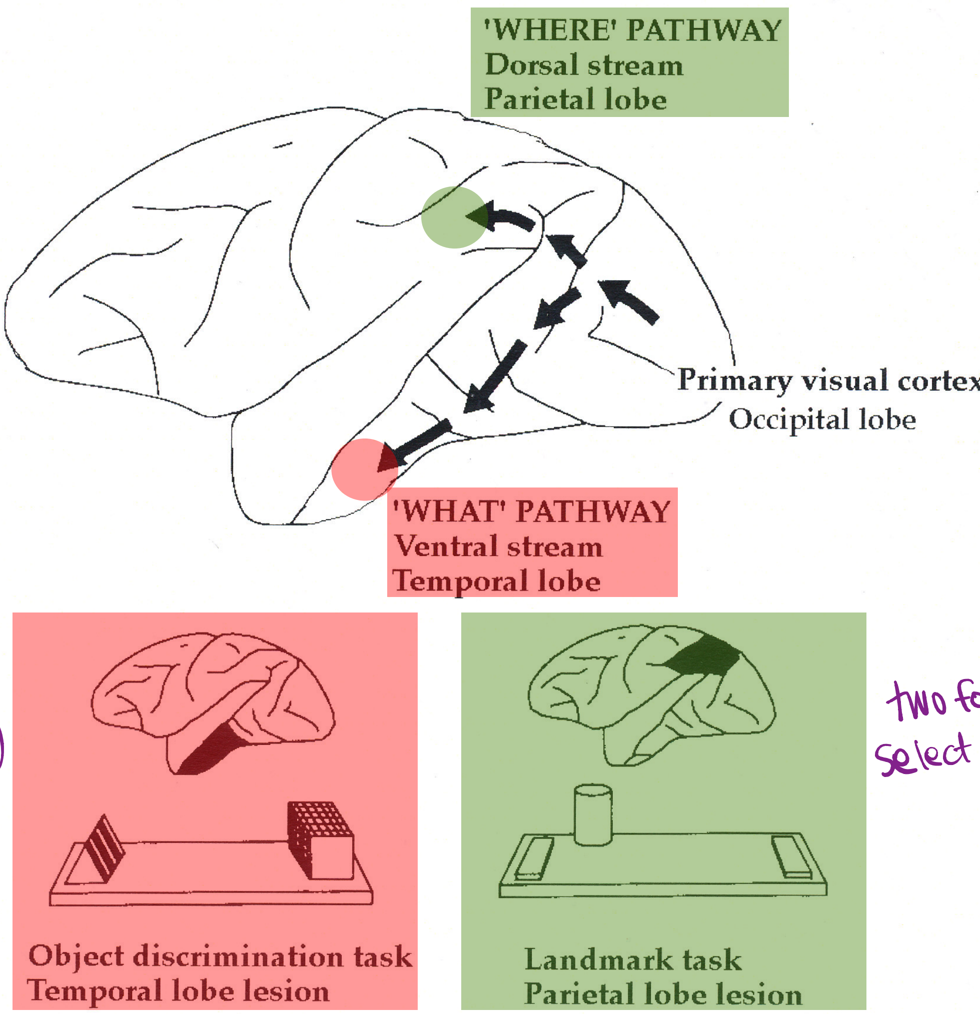
DORSAL STREAM



VENTRAL STREAM

The chain of connections leading outward from area V_1 to areas of progressively higher order bifurcates into a dorsal "stream" leading to parietal cortex (PG) and a ventral "stream" leading to inferotemporal cortex.

Desimone & Ungerleider (1989) Handbook of Neuropsychology, Vol. 2, Elsevier, pp. 267-299.



Select food well under covering

two food wells select closer to landmark

As first pointed out in a systematic way by Ungerleider and Mishkin, the dorsal and ventral stream areas seem to subserve spatial-motor and object-recognition aspects of vision respectively.

Akinetopsia

The visual disorder complained of by the patient was a loss of movement vision ~~in~~ all three dimensions. She had difficulty, for example, in pouring tea or coffee into a cup because the fluid appeared to be frozen, like a glacier. In addition, she could not stop pouring at the right time since she was unable to perceive the movement in the cup (or a pot) when the fluid rose. Furthermore the patient complained of difficulties in following a dialogue because she could not see the movements of the face and, especially, the mouth of the speaker. In a room where more than two other people were walking she felt very insecure and unwell, and usually left the room immediately, because 'people were suddenly here or there but I have not seen them moving'. The patient experienced the same problem but to an even more marked extent in crowded streets or places, which she therefore avoided as much as possible. She could not cross the street because of her inability to judge the speed of a car, but she could identify the car itself without difficulty. 'When I'm looking at the car first, it seems far away. But then, when I want to cross the road, suddenly the car is very near.' She gradually learned to 'estimate' the distance of moving vehicles by means of the sound becoming louder.

Unable to perceive the movement in a cup when the fluid rose

Could not see the movements of the mouth of the speaker

First the car seems far away, then it's very near

The visual disorder complained of by the patient was a loss of movement vision in all three dimensions. She had difficulty, for example, in pouring tea or coffee into a cup because the fluid appeared to be frozen, like a glacier. In addition, she could not stop pouring at the right time since she was unable to perceive the movement in the cup (or a pot) when the fluid rose. Furthermore the patient complained of difficulties in following a dialogue because she could not see the movements of the face and, especially, the mouth of the speaker. In a room where more than two other people were walking she felt very insecure and unwell, and usually left the room immediately, because 'people were suddenly here or there but I have not seen them moving'. The patient experienced the same problem but to an even more marked extent in crowded streets or places, which she therefore avoided as much as possible. She could not cross the street because of her inability to judge the speed of a car, but she could identify the car itself without difficulty. 'When I'm looking at the car first, it seems far away. But then, when I want to cross the road, suddenly the car is very near.' She gradually learned to 'estimate' the distance of moving vehicles by means of the sound becoming louder.

Normal:

- Visual acuity
- Stereopsis
- Color vision
- Recognition
- Word reading
- Flicker fusion
- Double simultaneous detection
- Saccadic localization
- Tactile motion
- Acoustic motion

Middle Temporal Gyrus

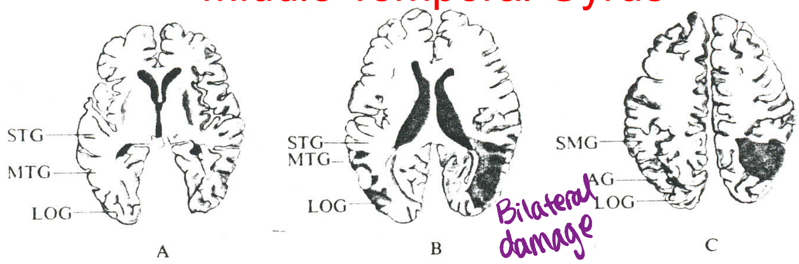


FIG. 1. Diagrams derived from axial CT scans arranged in sequence from A (low ventricular level), through B (high ventricular level) to C (supraventricular level). Hypodense lesions are marked in different shades of grey (slight hypodensities in light dotted grey, marked hypodensities in dark cross-hatched grey. The right-sided lesions are more extensive and more severe than the left-sided lesions. In slice B, a bean-shaped patch is shown on the left side, representing a 'cord sign', which is taken as evidence of venous thrombosis. AG = angular gyrus; LOG = lateral occipital gyri; MTG = medial temporal gyrus; SMG = supramarginal gyrus; STG = superior temporal gyrus.

Impaired

- Motion detection
- Direction discrimination
- Ocular pursuit
- Motion Aftereffect

Trouble seeing rapid motion

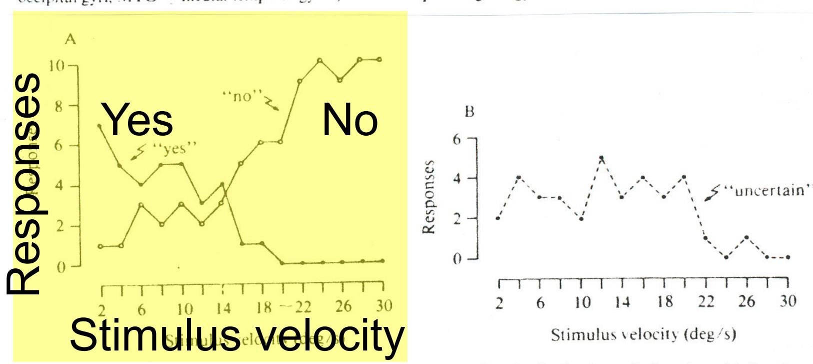
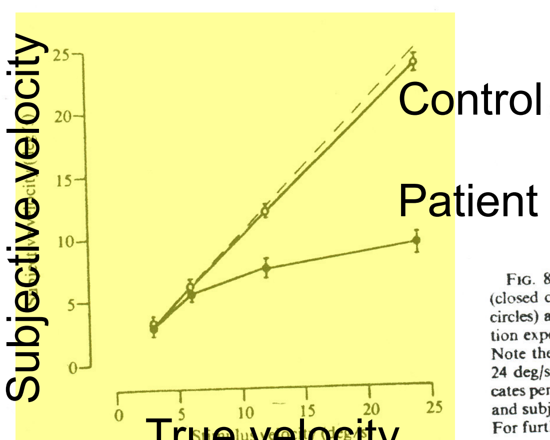


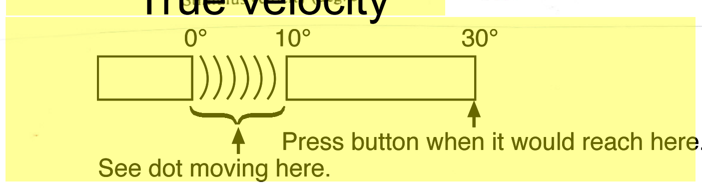
FIG. 5. A, number of 'movement' responses for a target moving in the horizontal direction. 'Yes' = clear movement vision, 'No' = no movement vision. B, 'uncertain' responses (i.e. no clear movement vision).

Control has good estimate of speed

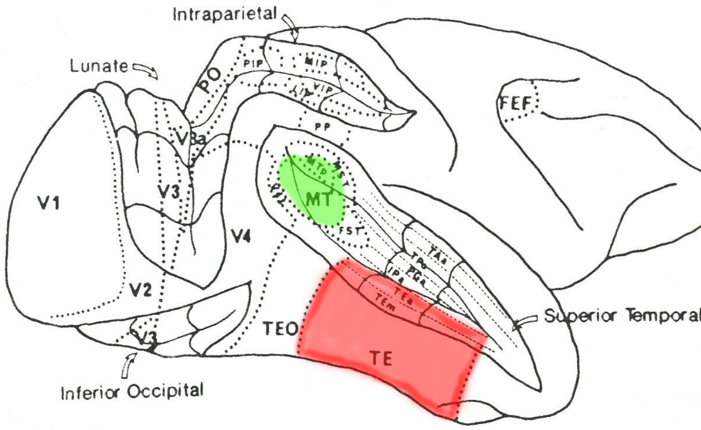


Selective deficits of motion perception have been observed, rarely, after temporal lobe injury in humans.

FIG. 8. Subjective velocity for the patient (closed circles) and the normal subject (open circles) as calculated from the motion prediction experiment (n = 10 trials per condition). Note the patient's underestimation of 12 and 24 deg/s stimulus velocity. Dashed line indicates perfect correspondence between stimulus and subjective velocity. Vertical bars: ±1 SD. For further details, *see text*.



Zihl et al.
Brain 106: 313-340 (1983)



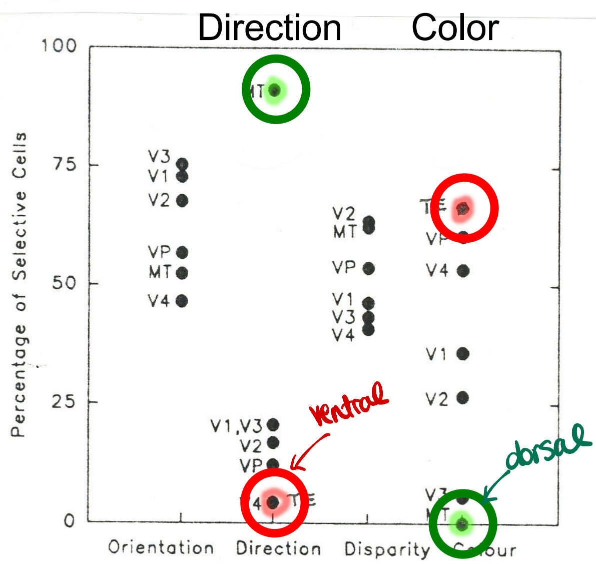
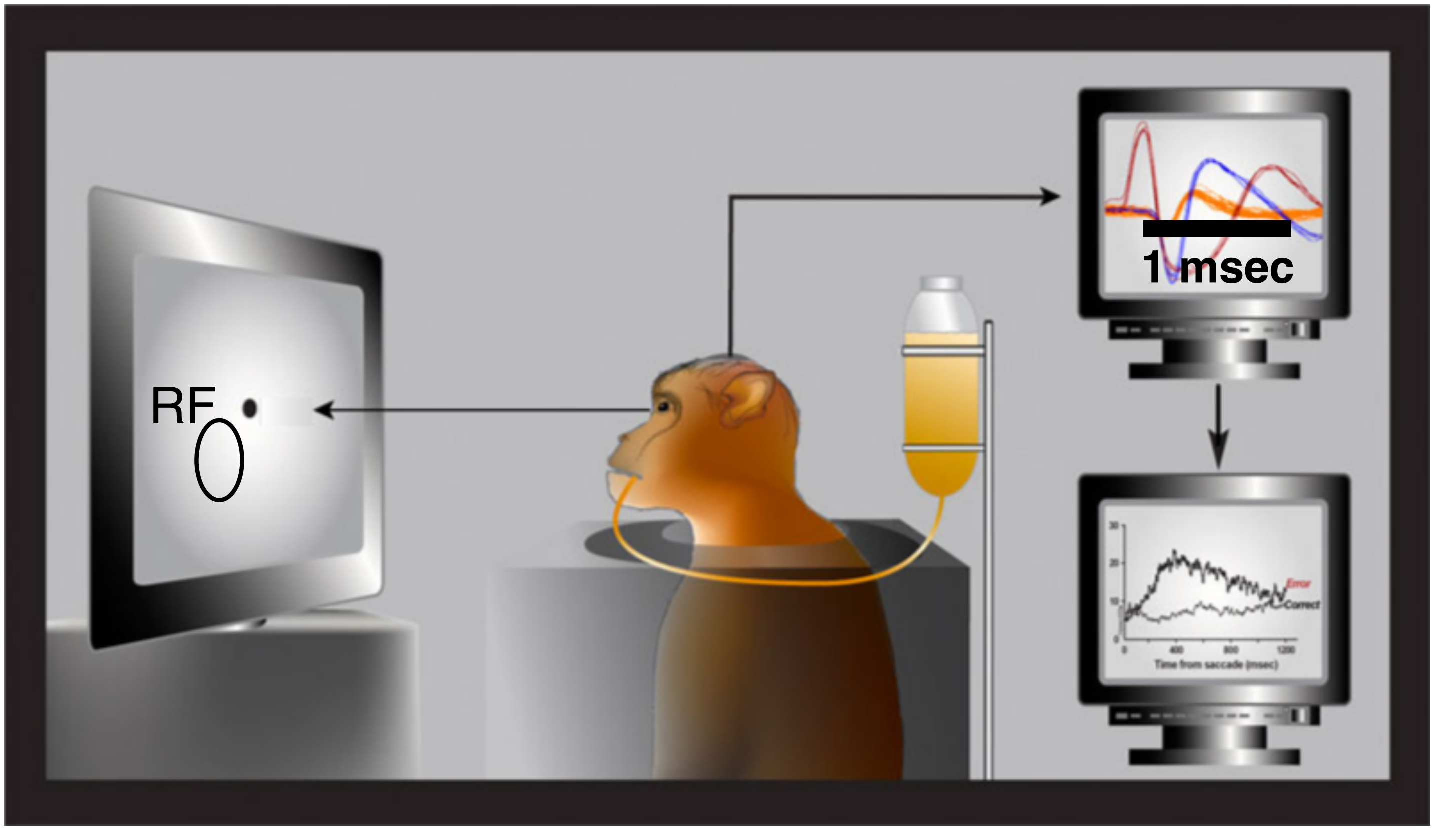


Fig. 1. The percentage of cells in six cortical visual areas that are selectively tuned to orientation, direction of motion, retinal disparity, or colour. Each point is the mean of from 1 to 10 separate investigations. Note that neurons in Area MT (V5) are highly selective for direction of motion and not selective for colour whereas the opposite occurs for neurons in area V4. The points were calculated from the data presented by Felleman and Van Essen [20] and the figure is reproduced from Cowey [11], with permission.

Visual areas differ markedly in the degree to which their neurons are sensitive to different visual-stimulus dimensions. Note the opposite patterns of color and direction selectivity in areas MT & V4/TE. Points for TE are from other sources.

Cowey & Heywood
Behav. Brain Res.
71: 89-100 (1995)

That ventral stream areas (V4 and TE) are sensitive to color whereas a dorsal stream area (MT) is sensitive to motion fits with the idea that they subserve recognition and spatial vision.



* Recording eye movements
* Record w/ microelectrode
neuronal activity
→ map out receptive
field (& what stimulus)

APs
· Brief deviations
in voltage (~1ms)
· Can hear them
(popcorn in pan)

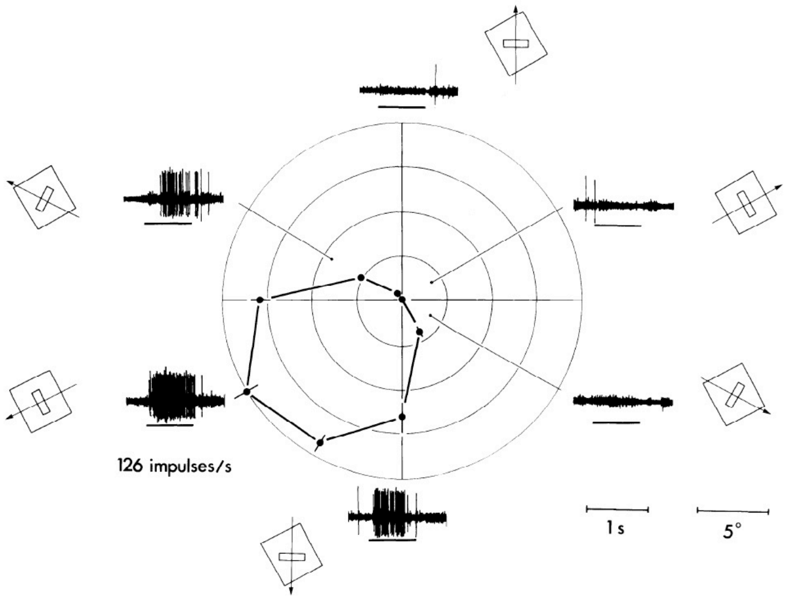
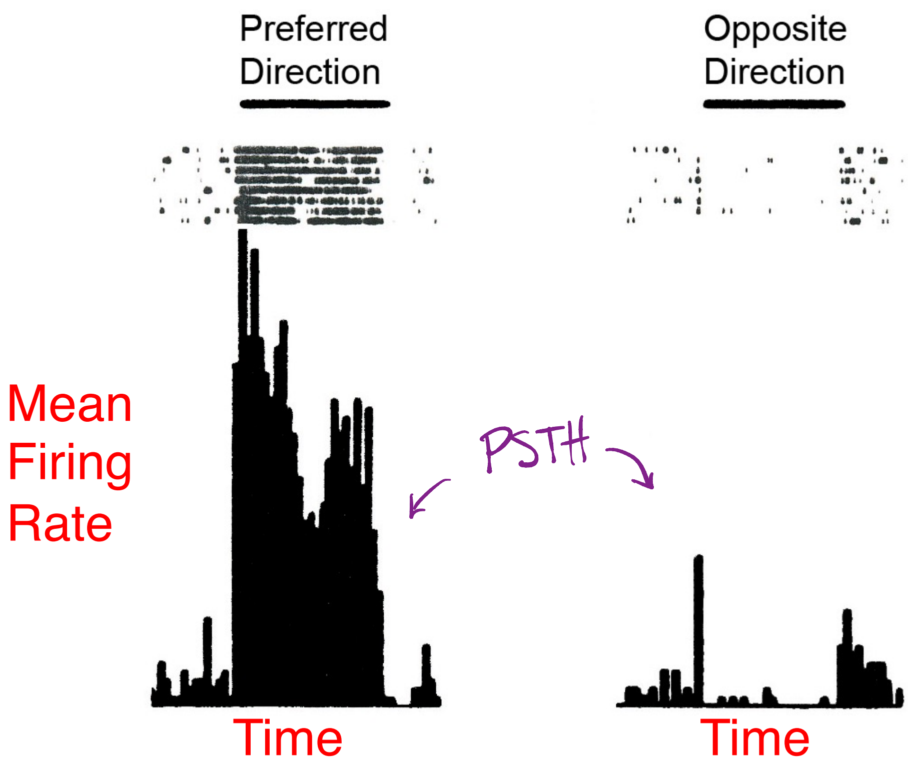


FIG. 1. Direction selectivity of a single unit in MT. Oscilloscope records of extracellularly recorded responses are shown for individual presentations of the six indicated directions of motion. Bars below each trace mark the time the stimulus was on. The size of the stimulus and its direction of motion relative to the receptive-field outline are indicated alongside each trace. The polar plot is the average rate of firing during stimulus presentation for five repetitions of 12 directions of motion. Bars indicate the standard error of the mean for each point.



Maunsell and Van Essen
Journal of Neurophysiology
49: 1127 (1983)

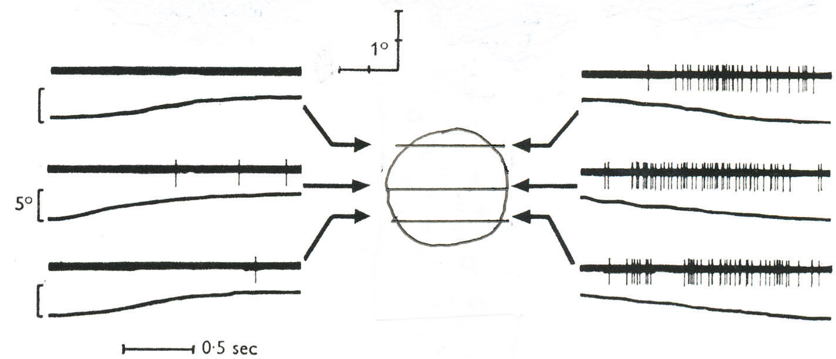


Fig. 3. Responses to motion along three different paths through the receptive field. The map in the centre shows the field and the paths through it; symbols as in Fig. 2. The records of the responses to traverses in the null direction are to the left, those for the preferred direction to the right. The lower trace of each pair is from a potentiometer and shows the position of the spot as it moved through the field (calibration at left). Top, middle and bottom parts of the receptive field all show the same directional selectivity.

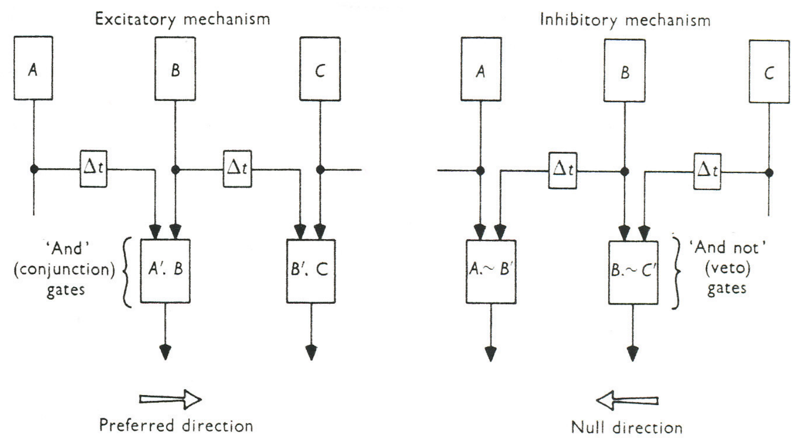
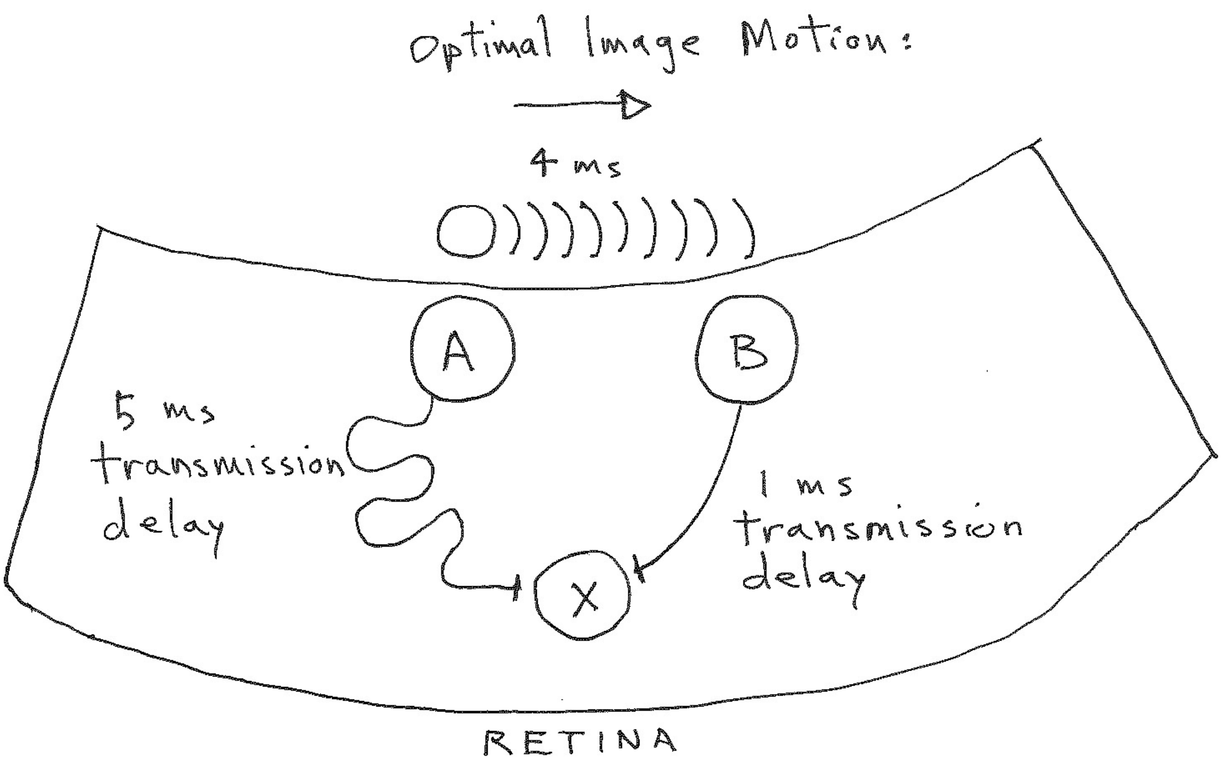


Fig. 7. Two hypothetical methods for discriminating sequence. For both, the preferred direction would be from left to right, null from right to left. In the excitatory scheme activity from the groups of receptors A and B is delayed before it is passed laterally in the preferred direction to the 'and' (conjunction) gates. If motion is in the preferred direction A' (delayed A) occurs synchronously with B, B' occurs synchronously with C, and these conjunctions cause the units in the next layer to fire. In the scheme on the right the activity spreads laterally, but in the null direction, from the groups of receptors B and C, and it has an inhibitory action at the units in the next layer; hence these act as 'and not' (veto) gates. The inhibition prevents activity from A and B passing through these gates if motion is in the null direction, but arrives too late to have an effect if motion is in the preferred direction. Notice that a special delay unit is not really necessary, for this scheme works if inhibition simply persists longer than excitation and can thus continue to be effective after a lapse of time. The excitatory scheme works by picking out those stimuli with the desired property, whereas the inhibitory scheme works by vetoing responses to unwanted stimuli; the latter is the one favoured by the experimental evidence.

In an influential 1965 paper, Barlow & Levick described neurons in rabbit retina selective for direction of motion & proposed a simple model to account for the phenomenon.

However, there is a big difference between detecting the motion of dots on the retina and representing perceived motion.

H.B. Barlow & W. R. Levick
J. Physiol. Lond. 178: 477-504 (1965)



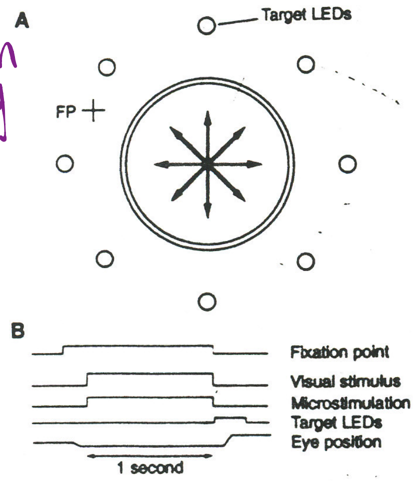
X fires most strongly when inputs from A & B hit it simultaneously.

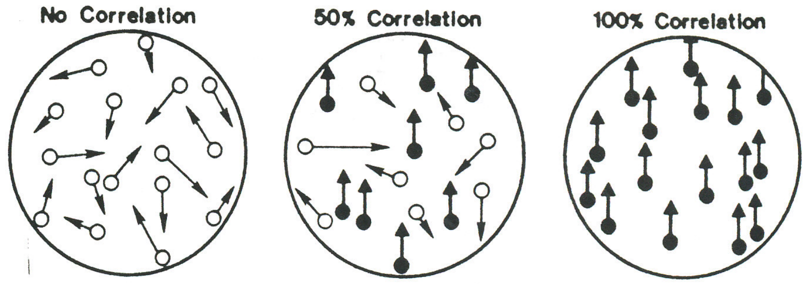
Direction-selectivity is ubiquitous

Why MT?

end of trial had to make saccade to target

What motion did monkey perceive?





Are behavioral and neuronal thresholds similar?

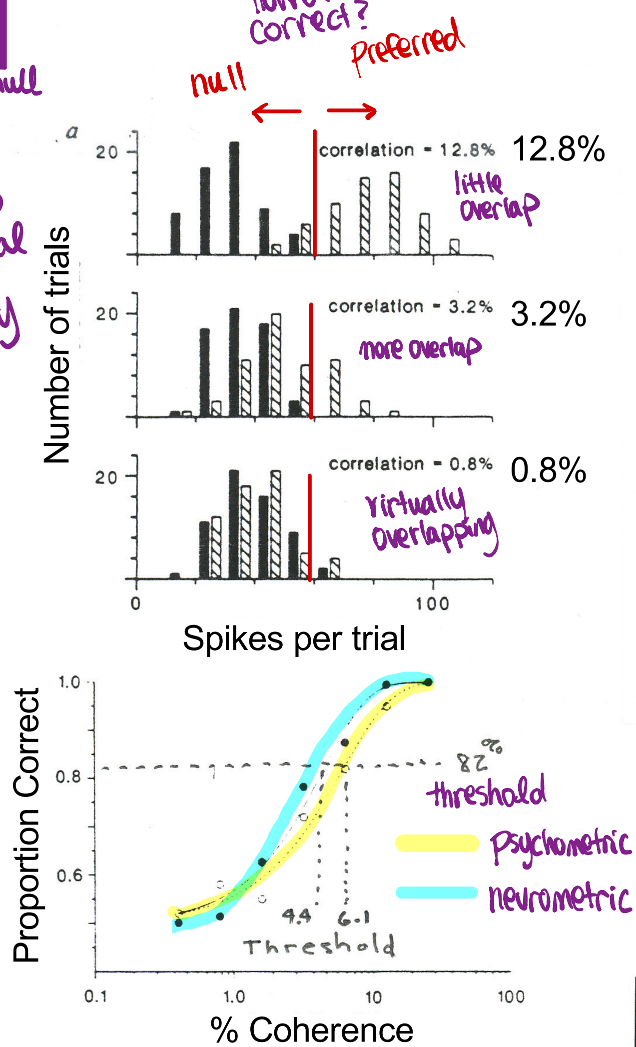
Newsome's task. While the monkey looks at a fixation point (FP), a moving-dot display with some degree of coherence is presented in the neuron's receptive field (double circle). The monkey must make an eye movement to the target toward which he thinks the motion flowed.

Coherence = fraction of dots moving in same direction

100% = all same
0% = random

How often correct?

Use LDA to find optimal decision boundary



a rhesus monkey. *a*, The responses of a directionally selective MT neuron at three different motion correlations spanning physiological threshold. The hatched bars represent responses to motion in the neuron's preferred direction; the solid bars indicate responses to motion in the null direction (180° opposite to the preferred). Sixty trials were performed in each direction for each of the three correlation levels. Response distributions for a range of correlation levels were used to compute a 'neurometric' function that characterized the neuron's sensitivity to the motion signal and could be compared with the psychometric function computed from the monkey's behavioural responses. *b*, Comparison of simultaneously recorded psychometric and neurometric functions. Psychophysical performance of the monkey. ○: performance of the neuron. ●. Psychophysical performance at each correlation is given by the proportion of trials on which the monkey correctly identified the direction of motion. Neuronal performance is calculated from distributions of responses like those in Fig. 1*a*, using a signal-detection method described in the text. The physiological and psychophysical data form similar curves, but the data for the neuron lie to the left of the data for the monkey, meaning that the neuron was somewhat more sensitive than the monkey. We fit the data with smooth functions of the form introduced to psychophysics by Quick[12]. Threshold, defined as the correlation for which the direction of motion was identified correctly on 82% of the trials, was 6.1% for the monkey and 4.4% for the neuron.

1/2 neuron better

1/2 monkey better

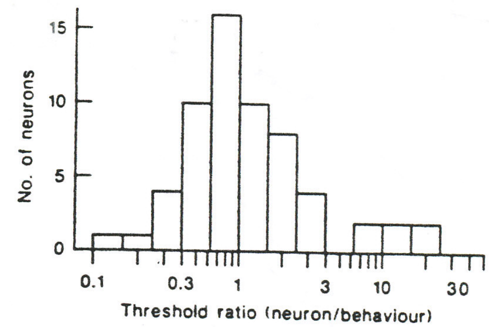


FIG. 2 Comparison of psychophysical and physiological thresholds obtained or 60 MT neurons in two rhesus monkeys. The frequency histogram shows he distribution of the ratio of the physiological threshold to the psychophysical threshold for all the neurons for which we obtained data. A value of 1 represents perfect correspondence between psychophysical and physiological thresholds; values <1 indicate that the physiological threshold was ower than the psychophysical threshold, whereas values >1 indicate the onverse. The directional preferences of the 60 neurons were roughly niformly distributed, and there was no reliable association between a euron's direction or speed preference and its threshold relative to the erceptual threshold.

Parallel

Correlated?

Similar

Changes in the percentage of correlated motion have closely parallel effects on perception (as indicated by behavioral report) and neuronal activity in MT.

Newsome et al.
Nature 341: 52-54
(1989)

\+ = pref dir
\- = null dir

Even when stimulus is constant, he reports better than average

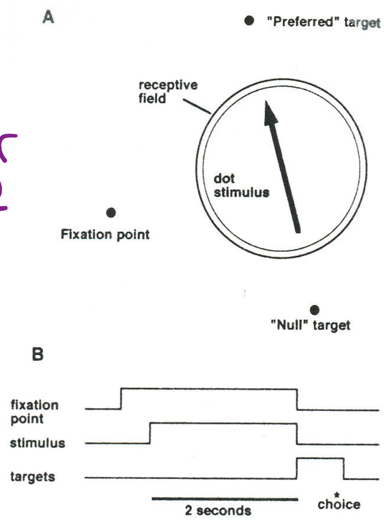


Fig. 1. Schematic of the behavioral task and stimulus configuration used in these experiments. A: Spatial configuration. The outer circle denotes the receptive field of the neuron under study, and the inner shaded region the random dot stimulus. This stimulus can be in either the neuron's preferred direction or its opposite ("null"). Response targets, which were small spots of light from projection LEDs, were aligned with the two possible directions of motion along a diameter of the stimulus. In some circumstances, we would shift these away from collinear alignment to reduce choice biases. B: Timing of events in a trial.

When there is no correlated motion and the monkey must guess, neuronal activity in MT is correlated with his guesses.

reported in pref dir
reported in null dir

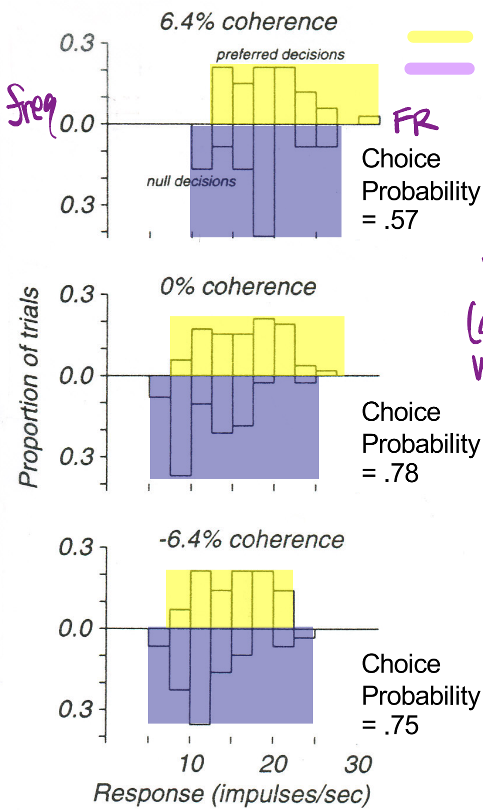
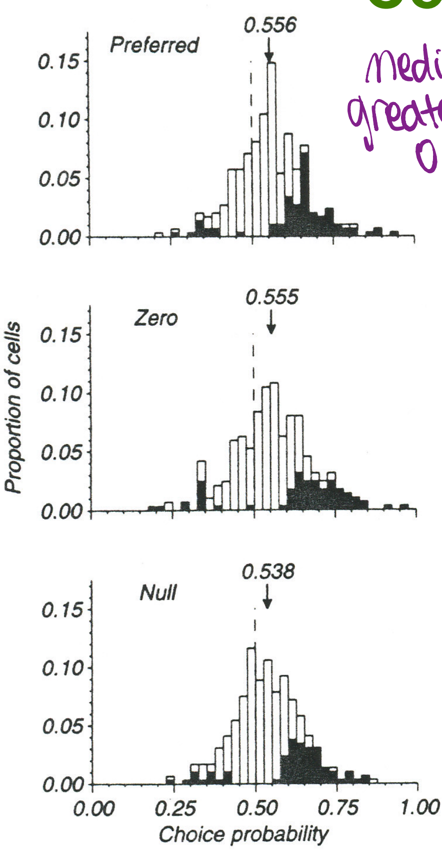


Fig. 2. Response distributions from a representative MT cell which showed a substantial trial-to-trial covariation between firing rate and behavior. Each panel represents a single stimulus coherence and direction; the −6.4% condition corresponds to null direction motion. The upper histograms (stippled) show firing rates on trials on which the monkey decided in favor of the preferred direction, and the lower histograms (open) show the firing rates on trials on which the monkey made the opposite decision.

You can guess (more than chance) which dir monkey reported

Correlated



median greater than 0.5

Fig. 5. Distributions of neuronal choice probability for all 299 cells in the sample, compiled separately for preferred direction (296 cases; a few lacked sufficient trials for analysis), null direction (293 cases), and zero coherence (287 cases) responses. Stippled bars indicate cases that were significantly different from 0.5 by the permutation test described in the text.

Used frozen noise

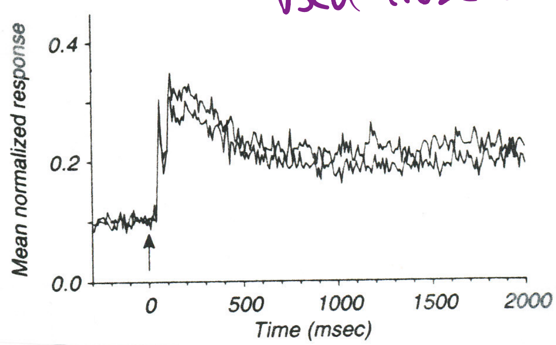


Fig. 11. Time course of the firing rate difference that underlies the choice probabilities. The 0% coherence responses of 75 cells that showed a significant choice probability were combined. Each cell gave a pair of averaged response histograms (bin width: 10 ms) corresponding to preferred and null direction decision trials. Each pair was normalized to the peak of the preferred direction histogram. A: Pooled average response histograms for each response direction, with the upper representing the preferred direction decision trials and the lower showing the null direction decision trials. B: The difference between the two responses as a function of time. Note that the response difference is only present during the visual stimulus period, and not during the fixation period prior to stimulus onset (arrows).

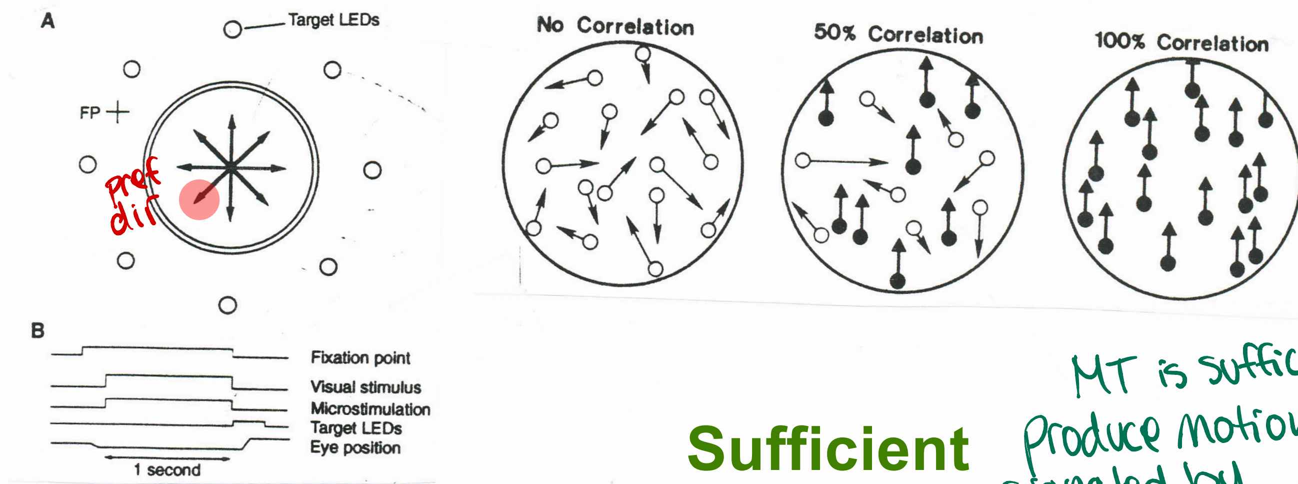
Britten et al. Vis. Neurosci. 13: 87-100 (1996)

Neuronal activity in MT is correlated w/ report w/ constant stimulus

But is MT proficient?

Electrical Stimulation

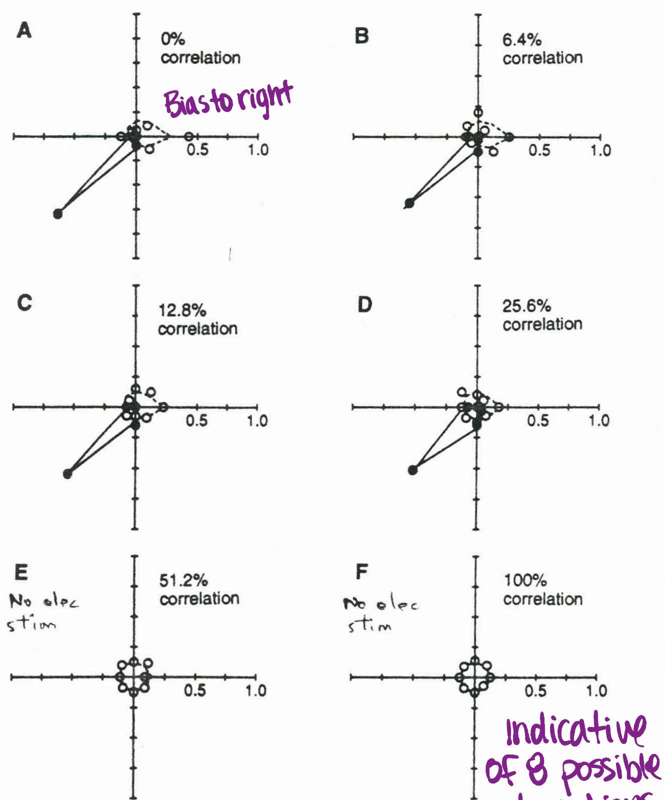
- Activating neurons in the neighborhood
- Pref dir is same down the column



Sufficient

MT is sufficient
Produce motion signaled by active neurons

O = no stim
● = elec stim



Indicative of 8 possible directions

Fig. 2. Polar plots showing monkey performance (circles) and model predictions (lines) for an eight-alternative microstimulation experiment. The preferred direction of neurons at this stimulation site was down and to the left. The data have been collapsed across visual stimulus direction so that one polar plot describes all choices made at a particular correlation. Open circles, performance on nonstimulated trials; closed symbols, the data from stimulated trials. Dashed lines, model predictions for nonstimulated data; solid lines, predictions for stimulated data. Data predicted by the model are at the vertices of each of the line plots; the vertices are connected with lines only for the purpose of presentation. Microstimulation was not applied at 51.2 percent and 100 percent correlation, and therefore only data and predictions for the nonstimulated condition appear. Eighty trials were performed at each correlation value.

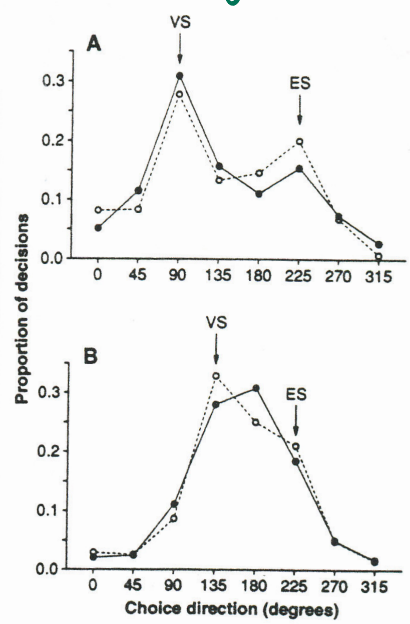


Fig. 3. The pattern of decisions made when the visual stimulus (VS) differed by (**A**) 135 or (**B**) 90 degrees from the preferred direction of the microstimulation effect (ES). Open symbols, the average proportion of the decisions made in each of eight response directions; closed symbols, model predictions for the same data points. Before averaging the selected data, each data set was rotated so that the preferred direction of the microstimulation effect corresponded to 225 degrees. The data were also symmetrically folded over so that visual stimulus motion clockwise to the microstimulation effect direction could be represented on the same plots as motion counterclockwise.

Electrical stimulation of a site in MT where neurons respond to motion in a certain direction sways the monkey's perception toward that direction.

Salzman & Newsome
Science 264:231-237
(1994)

Is it necessary?

Lesion experiment

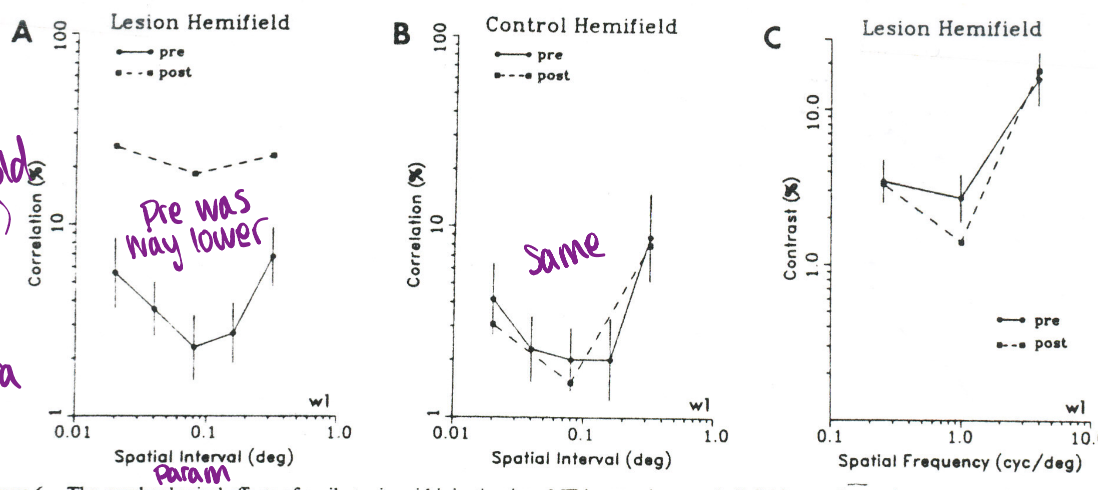
Map MT in one hemisphere

threshold (82%)

Sensitivity ↓ on side contra to lesion

Pre was way lower

Same



Param

Figure 6. The psychophysical effects of an ibotenic acid injection into MT in experiment *w1*. *Solid line and error bars* in *A–D* indicate the mean prelesion threshold and standard deviation for each condition tested; *dashed line*, postlesion thresholds obtained 24 hr after the MT injection. *A*, Motion thresholds for 5 different spatial intervals in the test (contralateral) hemifield. Again, the MT lesion caused striking elevations of motion thresholds in the test hemifield. *B*, Motion thresholds were within the normal range in the control (ipsilateral) hemifield. *C*, The MT injection had no effect on contrast thresholds in the test hemifield.

~ Necessary

Compelling correlation b/t motion perception & neuronal activity in MT

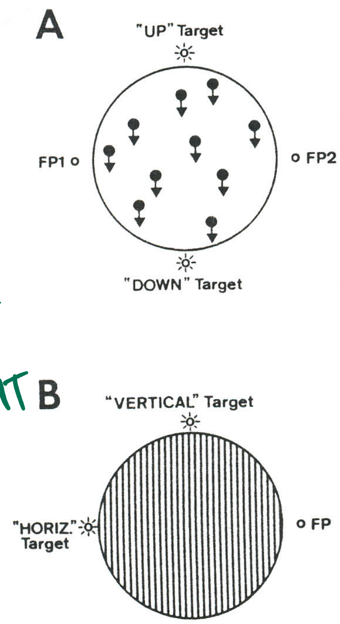


Figure 2. Behavioral paradigms employed for measuring psychophysical thresholds. *A*, For motion thresholds, the monkey viewed a dynamic random dot pattern that appeared within a circular aperture. Net motion of the dot pattern was either upward or downward for a given trial. The monkey fixated a point of light at location FP1 or FP2 while viewing the dot pattern perifoveally for 2 sec. At the end of the viewing interval, the fixation point vanished and 2 saccade targets appeared, one above the viewing aperture and the other below. The monkey was required to make a saccade to the target that corresponded to the direction of motion of the dot pattern ("UP" or "DOWN" target). A correct choice was rewarded with a drop of water. The intensity of the motion signal (percentage correlation) was varied from trial to trial in order to measure the threshold intensity for which the monkey could successfully discriminate the direction of motion. The fixation point was randomly alternated between locations FP1 and FP2 so that thresholds could be measured simultaneously in each hemifield (see text). *B*, For contrast thresholds, the monkey viewed a stationary sine wave grating through the same aperture employed during measurement of motion thresholds. Again, the monkey was required to fixate a small target (e.g., FP) while viewing the stimulus aperture perifoveally. Following the 2 sec viewing period, the monkey indicated whether the grating was oriented vertically or horizontally by making a saccade to the corresponding target ("VERTICAL" or "HORIZONTAL" target). Grating contrast was varied from trial to trial in order to determine the threshold contrast for which the monkey could successfully discriminate the orientation of the grating.

Present but not perfect

gets better over time

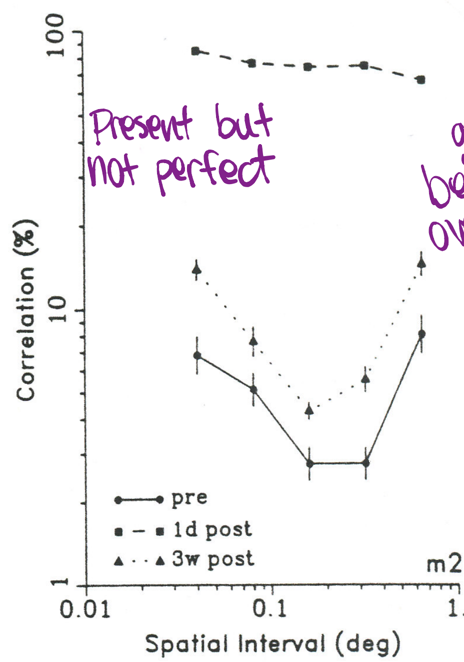


Figure 9. Recovery of function following a complete unilateral lesion of MT in experiment *m2*. *Solid line* indicates prelesion thresholds for this experiment; *dashed line*, postlesion thresholds obtained 24 hr after the second round of injections in this hemisphere; *dotted line*, postlesion thresholds 2–3 weeks postlesion. *Symbols* for the prelesion and the 3 week postlesion data represent the mean value of at least 10 threshold measurements for each condition; *error bars*, standard error of the mean. We tested this animal until 5 months postlesion, but observed little recovery beyond that evident at 3 weeks. The residual deficit thus appeared to be permanent.

Lesions of area MT in the monkey produce an impairment of motion perception.

Newsome & Paré
J. Neurosci. 8: 2201–2211 (1988)

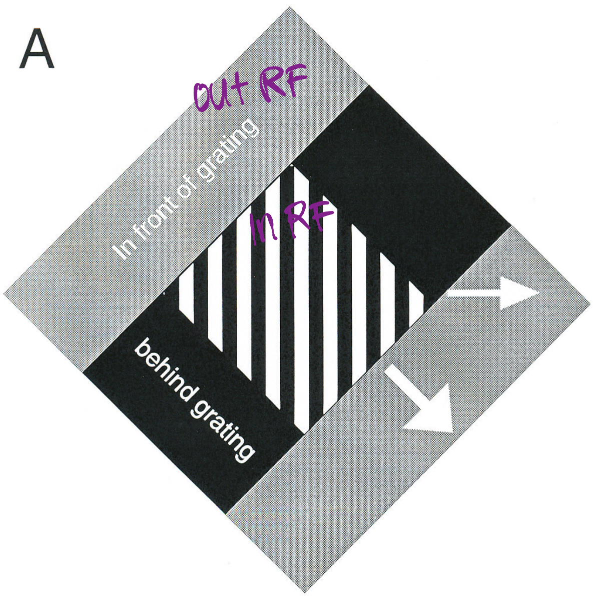
Retina vs. Motion Perception

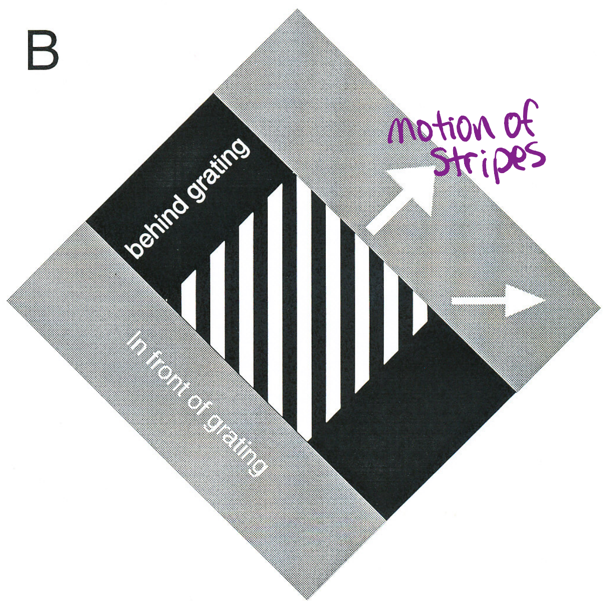
Barber diamond illusion

The small arrow indicates the direction of motion of the stripes (component direction) and the large arrow indicates the direction in which the pattern is perceived as moving (pattern direction). The panels surrounding the grating are not actually black and gray. Rather, they are textured surfaces on which depth is imposed by stereoptic cues. For a demonstration of this illusion, see http://www.cnl.salk.edu/~gene/ (you'll need red-green glasses).

Why does the illusion occur? It seems that, when one surface occludes another, the perceptual system decides that the nearer object "owns" the edge. The grating is perceived as owning two of its four edges - those where it overlies a still more distant surface. These owned edges consist of line terminators that are moving either down and to the right (A) or up and to the right (B). The perceived direction of motion of the grating coincides with the direction of motion of the line terminators that it owns.

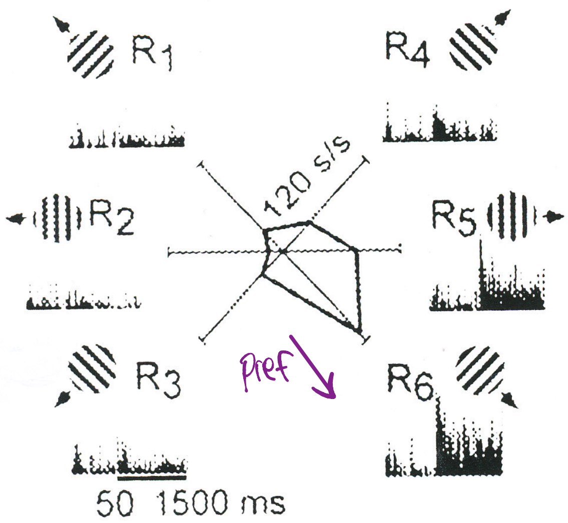
Research in Tom Albright's lab has shown that some neurons in MT encode the pattern as opposed to the component direction of motion in the barber diamond display. This is true even when the neuron's receptive field is entirely within the striped area. Thus the direction of motion signaled by MT neurons is not determined just by the pattern of motion on the retina. Quite the contrary, it reflects the direction in which an object is perceived as moving - as based on quite complex computations that involve parsing the scene into objects and deciding which objects occlude which others.





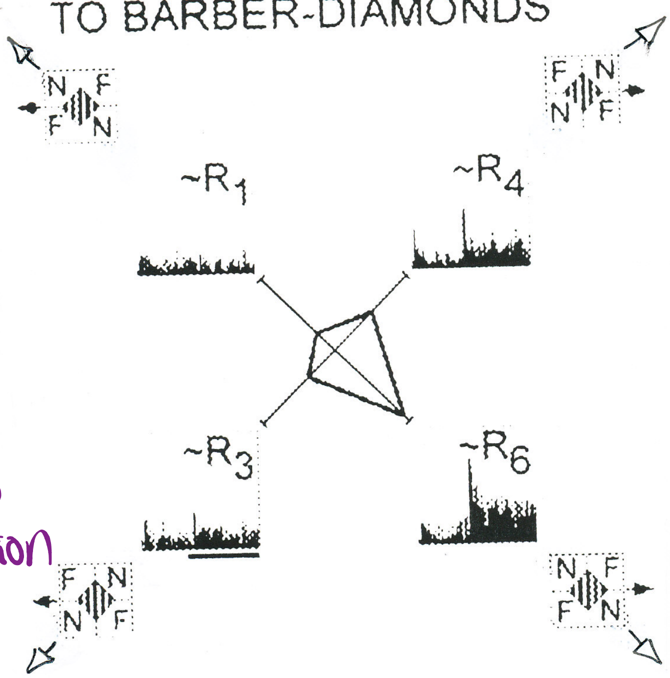
a) CIRCULAR GRATING RESPONSES

ideal task case



pref

b) ACTUAL RESPONSES TO BARBER-DIAMONDS



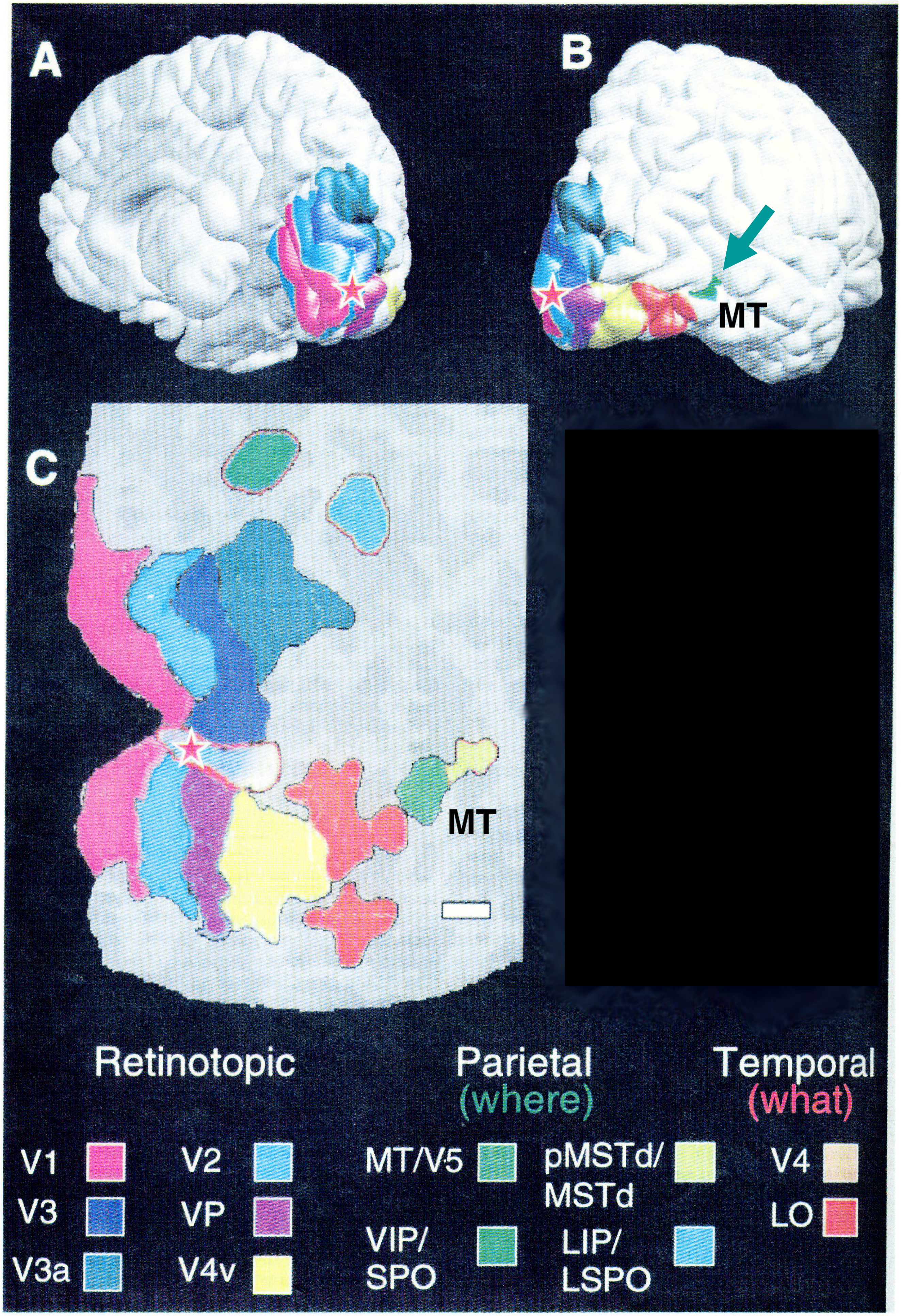
induce perception

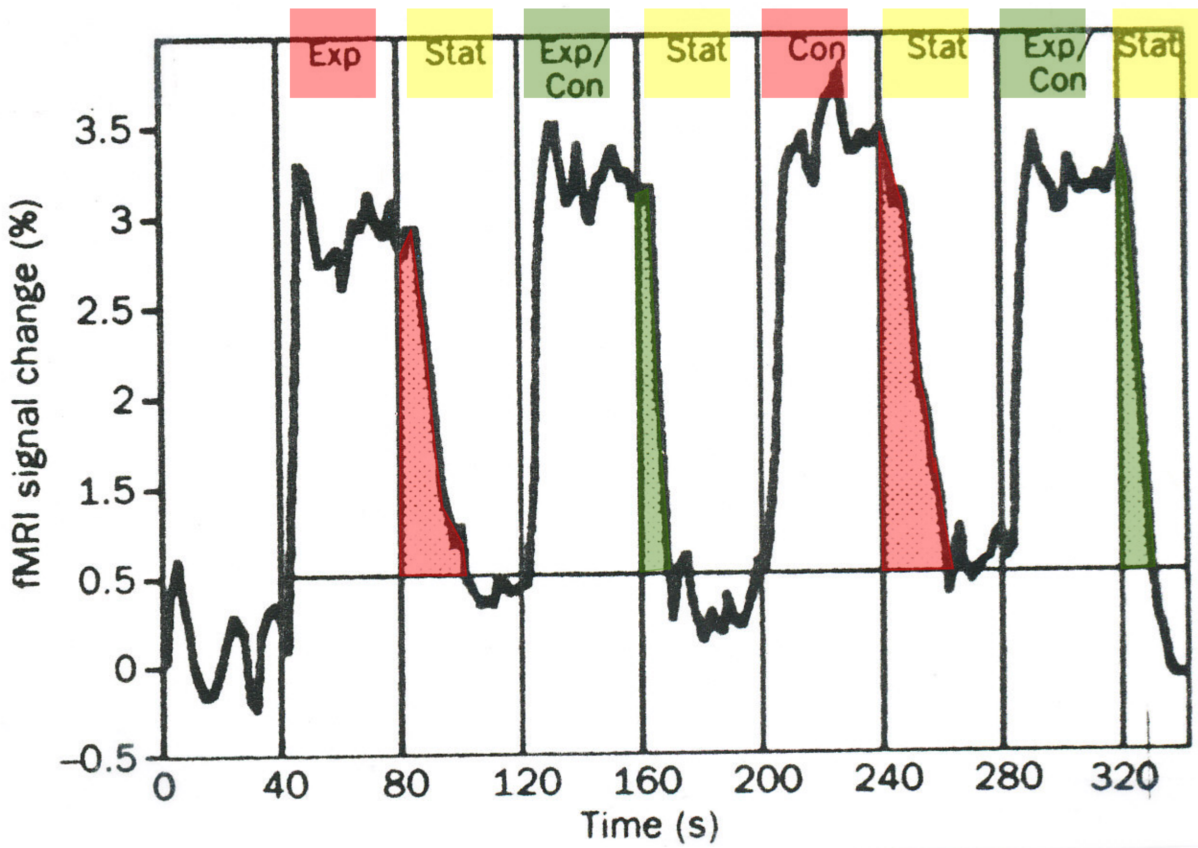
As context varies (illusion effect) neuron activity varies

Duncan, Albright & Stoner, J. Neurosci. 20: 5885-5897 (2000).

> Data from an MT neuron influenced by the direction of pattern motion in the Barber's Diamond display.
> N = Near surface } Relative to
> F = Far surface } viewer
> → = component motion
> ▷ = pattern motion

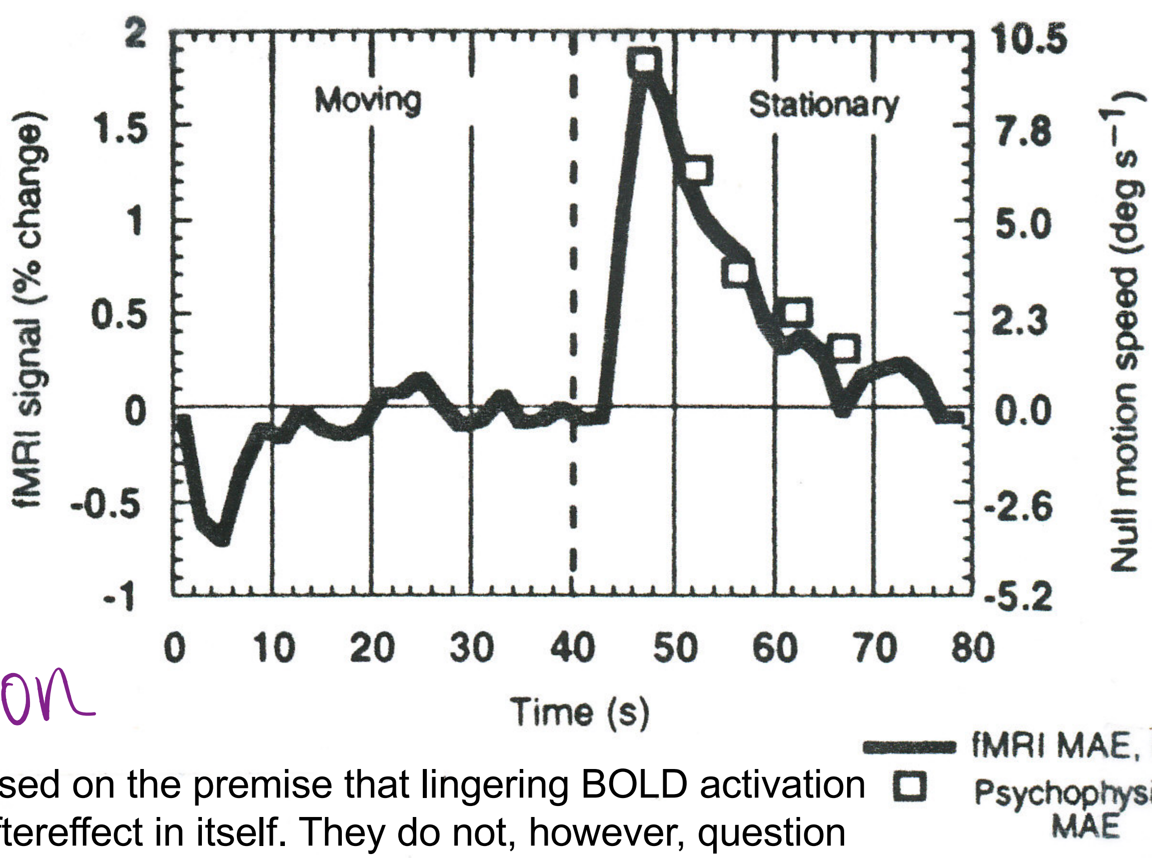
What about motion after effect?


A
B
MT
C
MT
Retinotopic
Parietal
(where)
Temporal
(what)
V1
V2
V3
VP
V3a
V4v
MT/V5
pMSTd/
MSTd
VIP/
SPO
LIP/
LSPO
V4
LO



Red minus Green

- - - - Offset of stimulus



Attention

ıis effect based on the premise that lingering BOLD activation
ıe motion aftereffect in itself. They do not, however, question
rons signaling the adapted direction and its opposite.

The BOLD response to a moving stimulus greatly exceeds the response to a stationary stimulus in MT but not V1 of humans. Tootell et al. J. Neurosci. 15: 3215-3230 (1995)

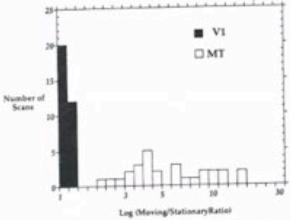
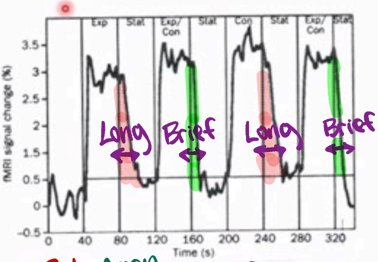


Figure 6. Variability in motion selectivity across scans. For each individual scan in which the radial motion-versus-stationary random dot stimuli were presented (e.g., Fig. 4), the percentage change in activity (moving/stationary) was sampled in MT and V1. Data were obtained from 32 scans in 13 subjects for V1, and 29 scans in 12 subjects (a subset of the V1 sample) for MT. In area V1, values were tightly clustered (range = 1.0–1.3). Values in MT were always more motion-selective than those in V1, but they were more variable (range = 2.0–16.1). The increased variability may reflect inadvertent partial volume sampling with adjacent areas of lesser motion selectivity, and/or the effects of slight changes in the numerator on the motion selectivity ratio.

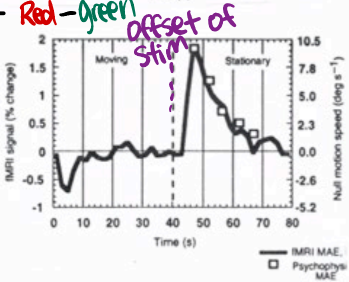
Time-course of the MT BOLD response to the following patterns of stimulation, each delivered for 20 sec:

Exp: Constantly expanding rings
Con: Constantly contracting rings
Exp/Con: Alternately expanding and contracting rings
Stat: Static rings

Note that activation persists for some time after Exp or Con. This likely is a correlate of MAE (motion aftereffect). Tootell et al. Nature 375: 139-141 (19



— Red - green



The BOLD "aftersignal" in MT (activation following EXP & CON minus activation following EXP/CON) closely parallels, in the time-course of its fall-off (black curve), the decay of the motion aftereffect as measured in psychophysical experiments (white squares).

Attention

Huk et al. Neuron 32(1): 161-172 offer an explanation for this effect based on the premise that lingering BOLD activation arises from attention to perceived motion as distinct from the motion aftereffect in itself. They do not, however, question the premise that MAE arises from differential activity in neurons signaling the adapted direction and its opposite.