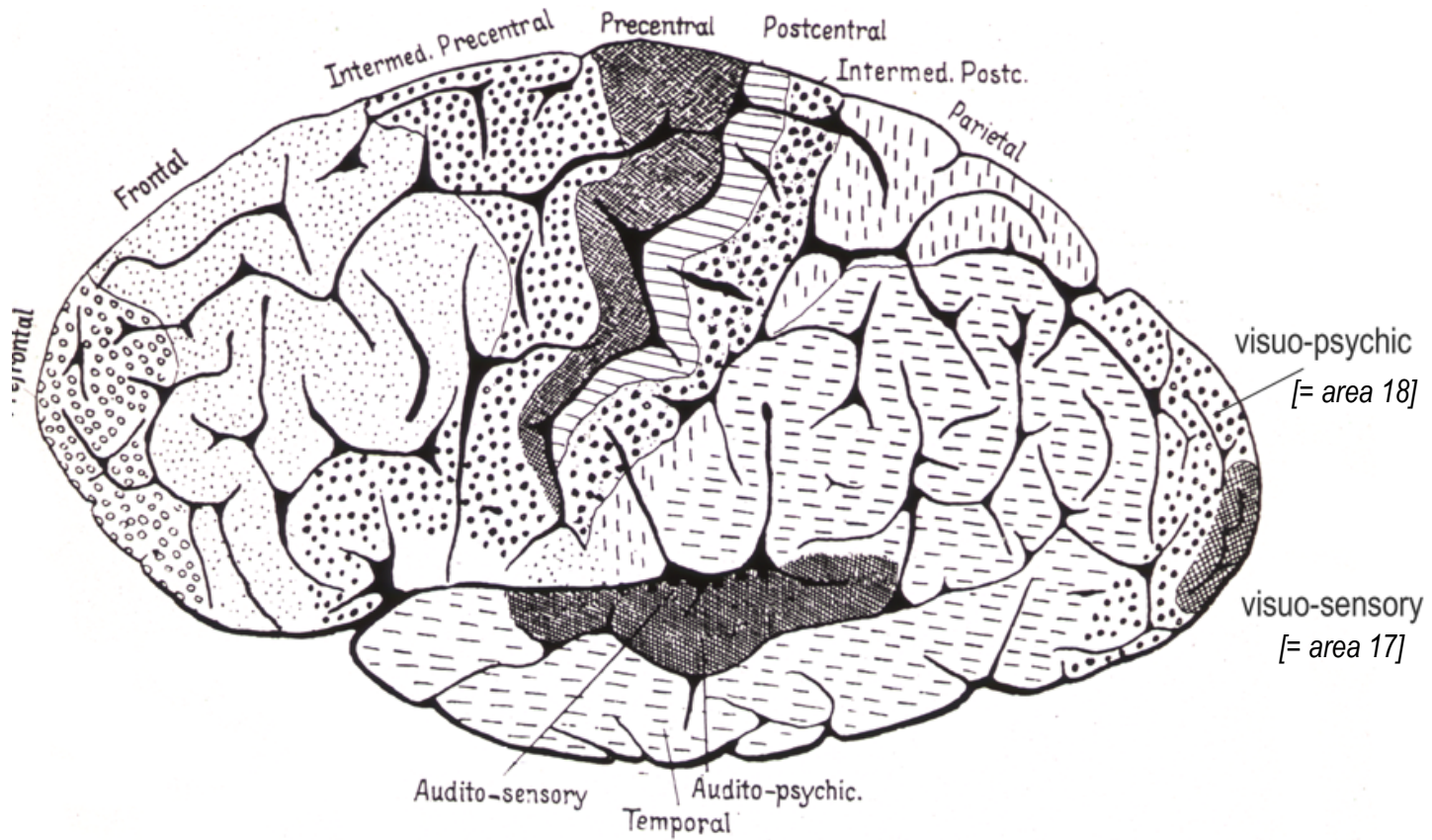


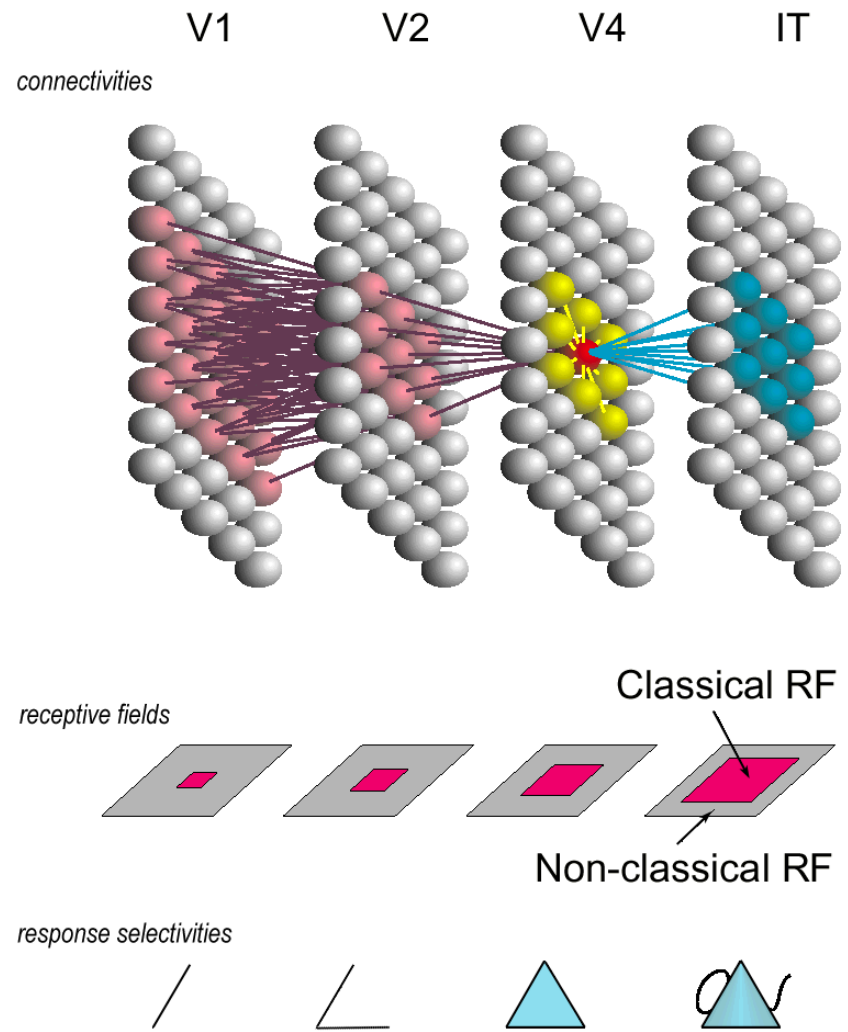
An elementary hierarchical theory of vision

Campbell 1905

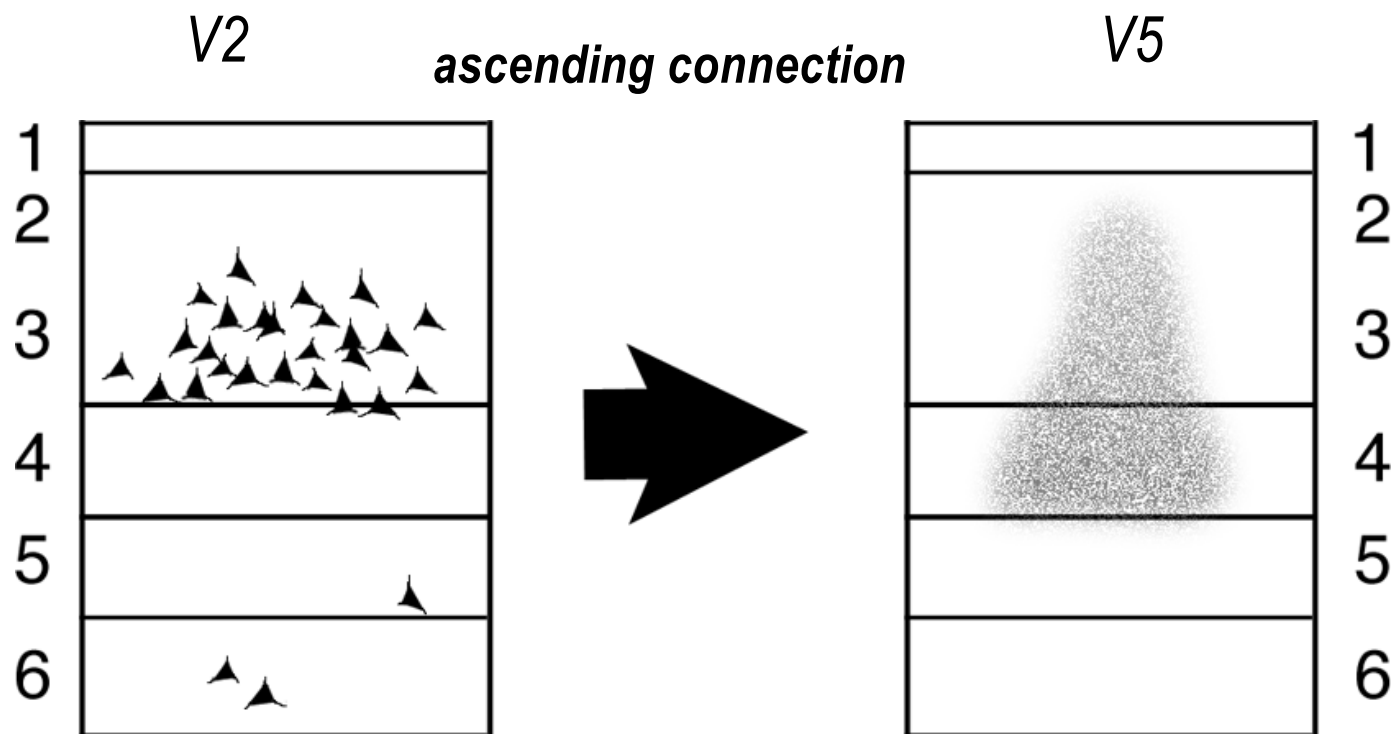


'What's up' in a serial pathway?

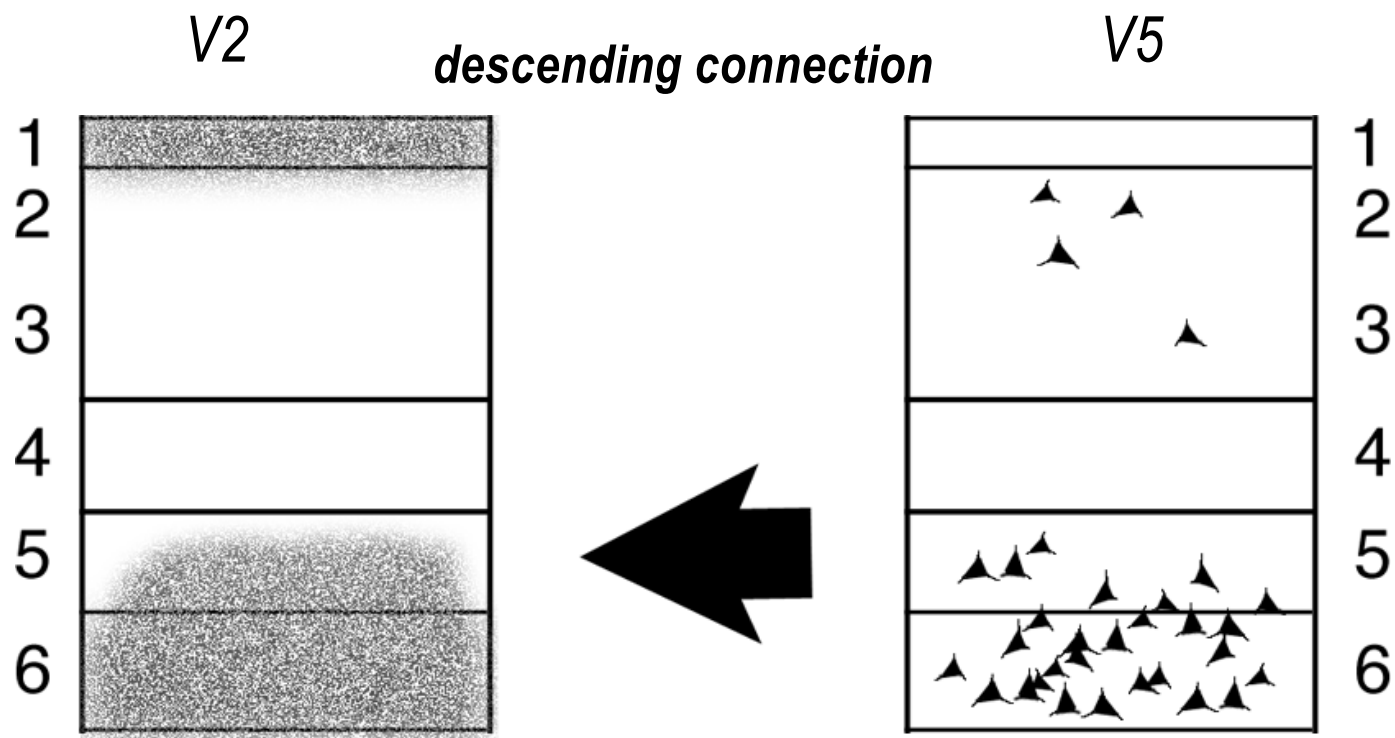
Lamme & Roelfsema (2000)



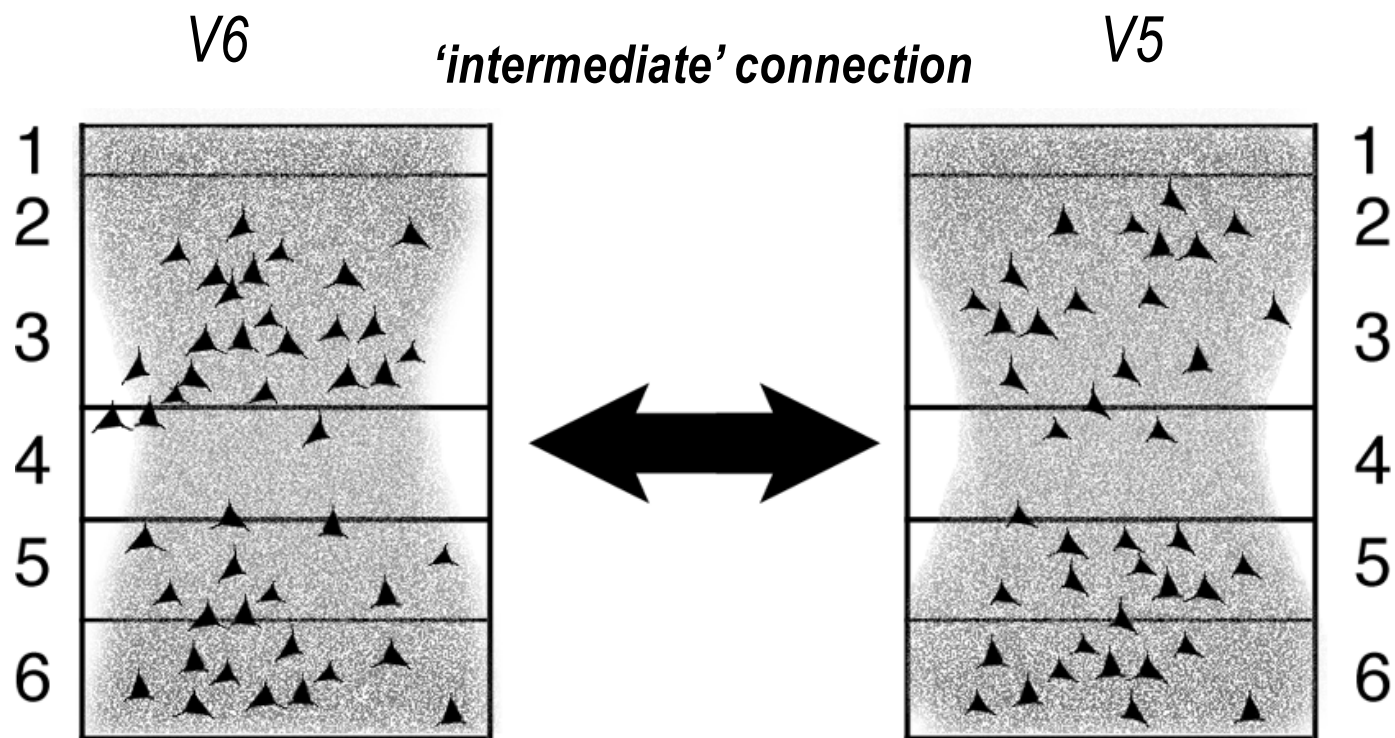
The laminar connectivity basis of hierarchical relationships between cortical areas



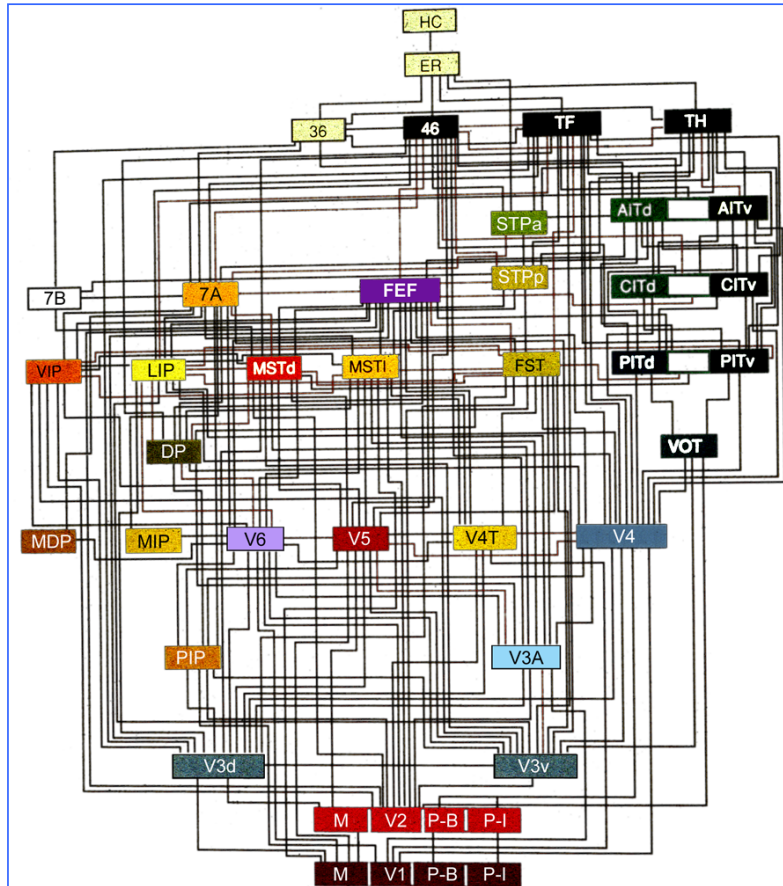
The laminar connectivity basis of hierarchical relationships between cortical areas



The laminar connectivity basis of hierarchical relationships between cortical areas



Felleman & Van Essen (1991) [ref. 1]



A systematic hierarchy can only be constructed if the 'rules' of laminar connectivity are universal:

1. Distinct patterns of termination:

*forward pathways terminate in layer 4
backward pathways terminate in layers 1 & 6.*

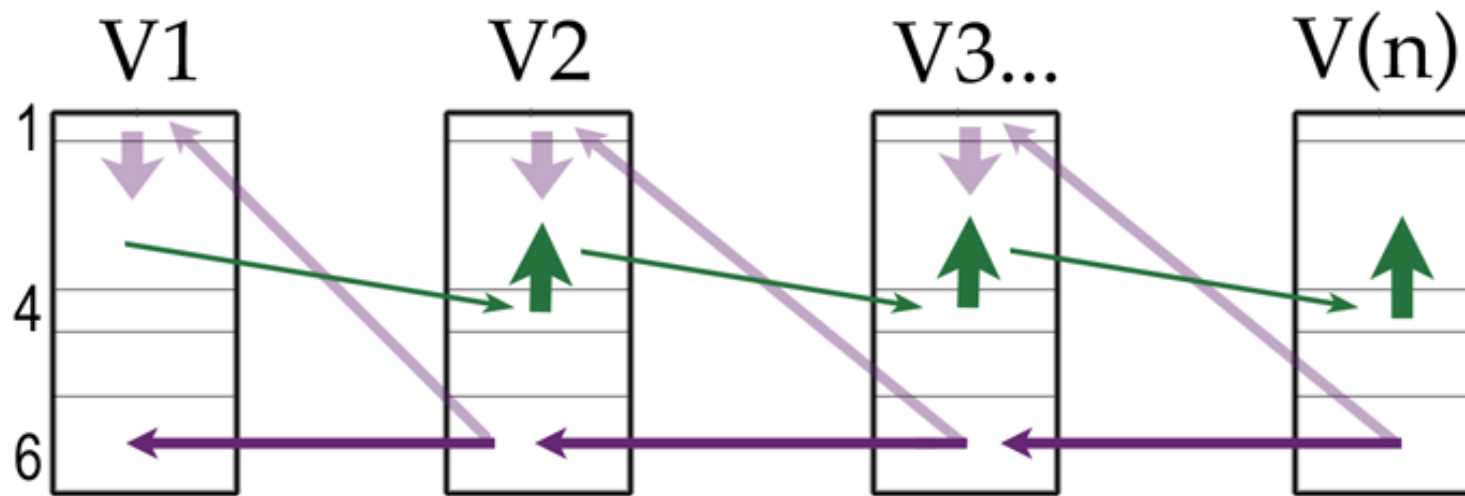
2. Reciprocity:

*if area 'A' sends a forward output to area 'B', then 'B' sends a backward output to 'A'.
- area B is termed a 'higher' area*

3. Transitivity:

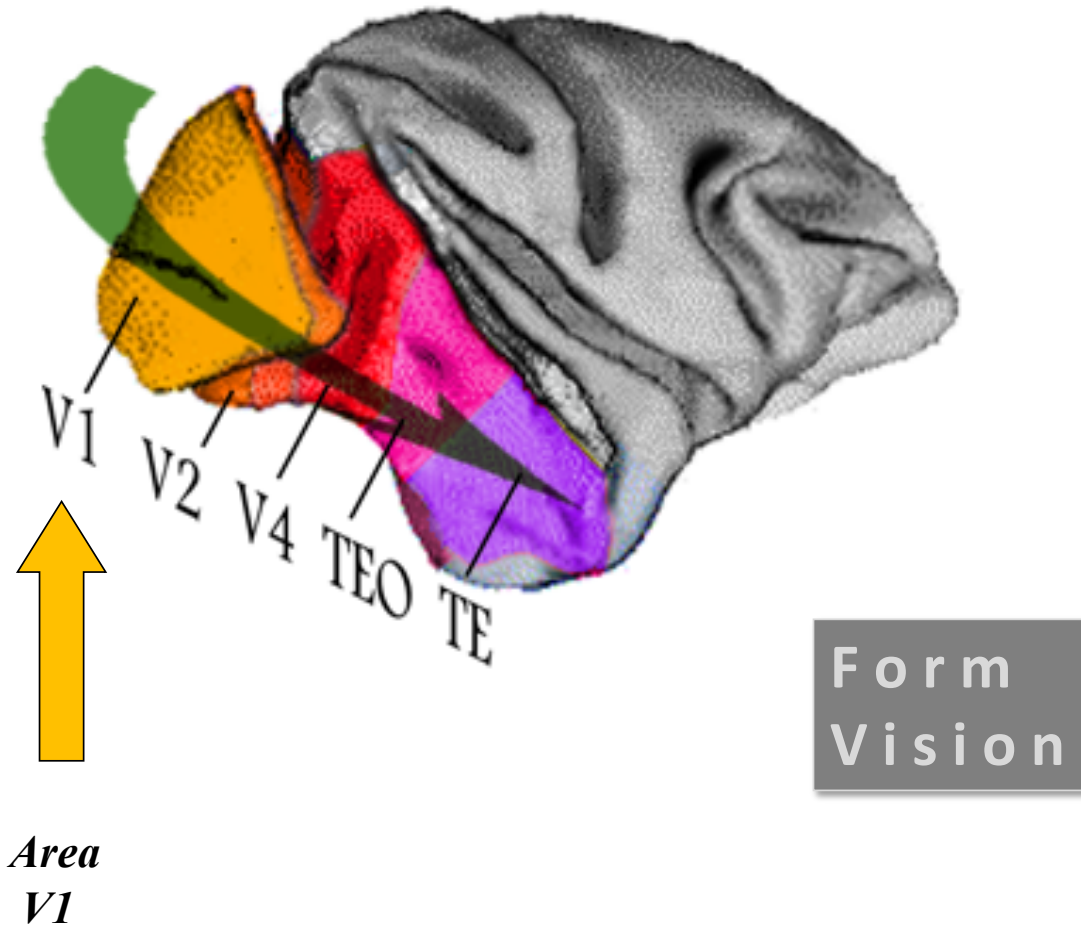
*if area 'B' is higher than area 'A',
and area 'C' is higher than 'B'
-- then area 'C' will also be found to be higher than 'A'.*

ascending pathways



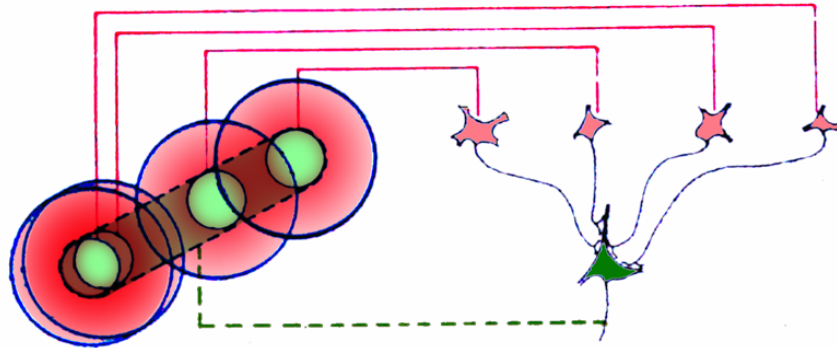
*descending pathways
(feedback)*

The ventral visual pathway... a chain of areas achieving object recognition



Hubel & Wiesel: hypothesis for construction of 'simple' and 'complex' receptive fields

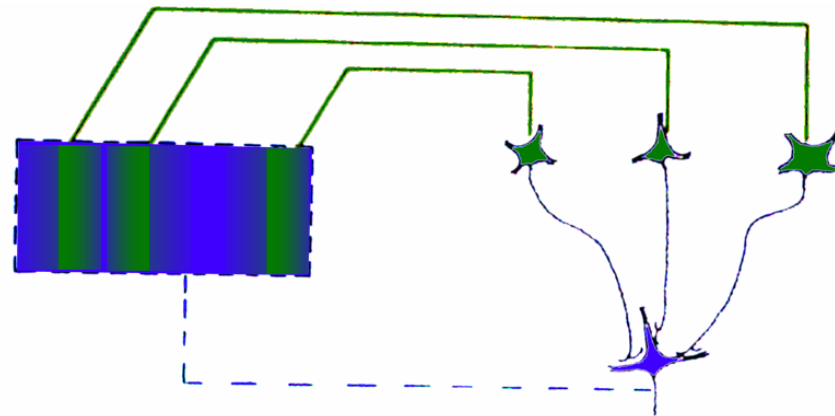
'simple' RF



concentric
(e.g. layer 4)

'simple' cell

'complex' RF

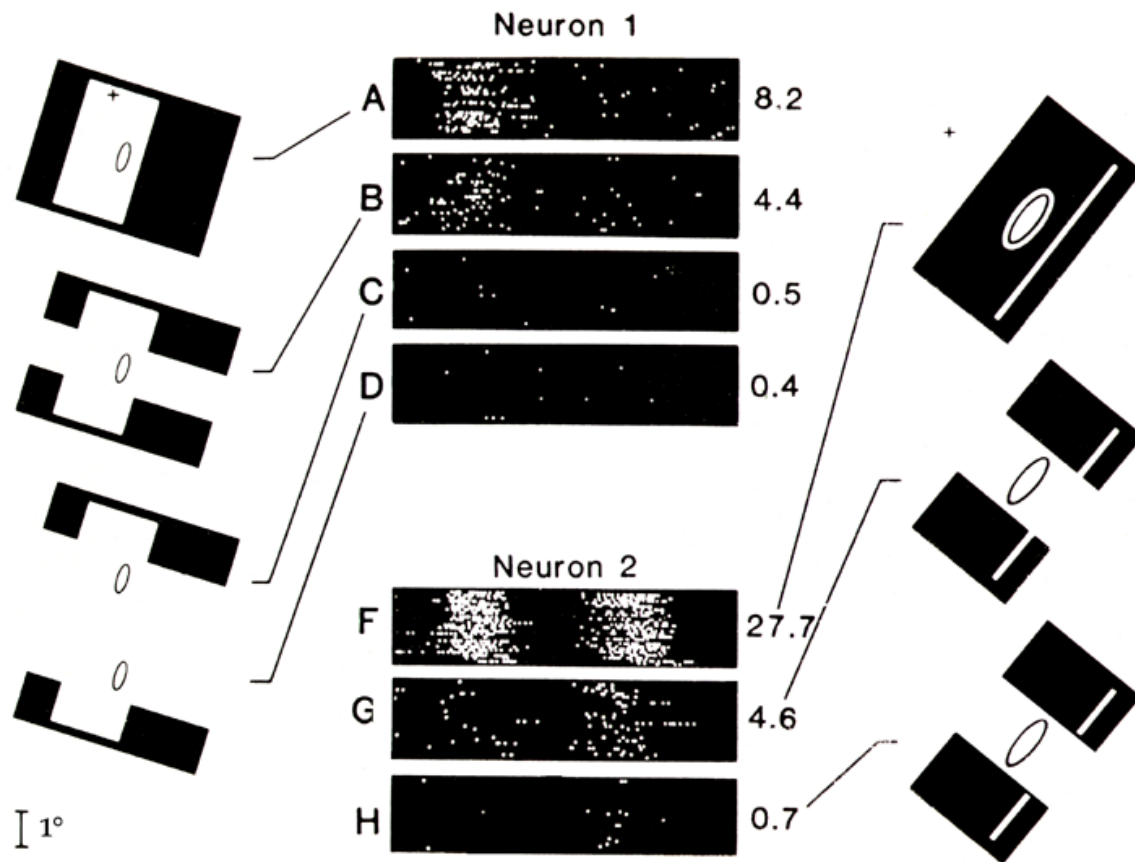


'simple' cells

'complex' cell

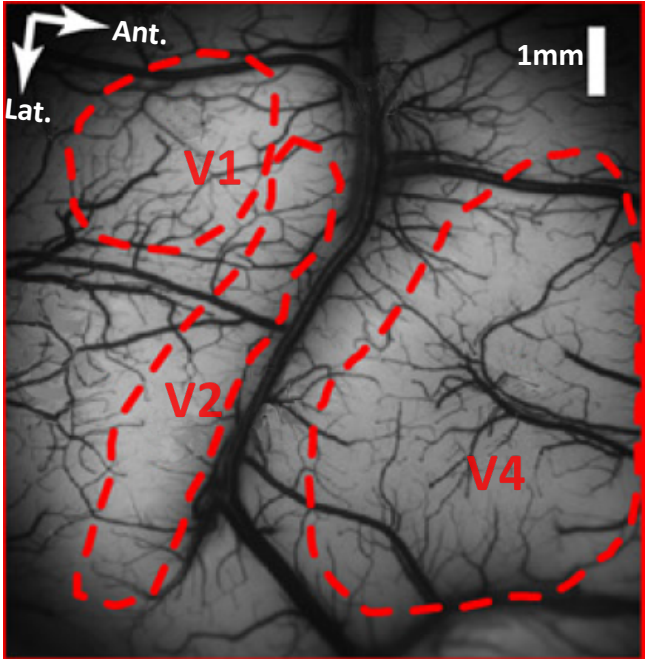
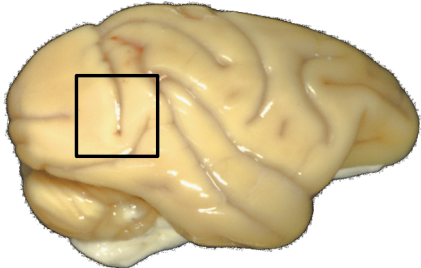
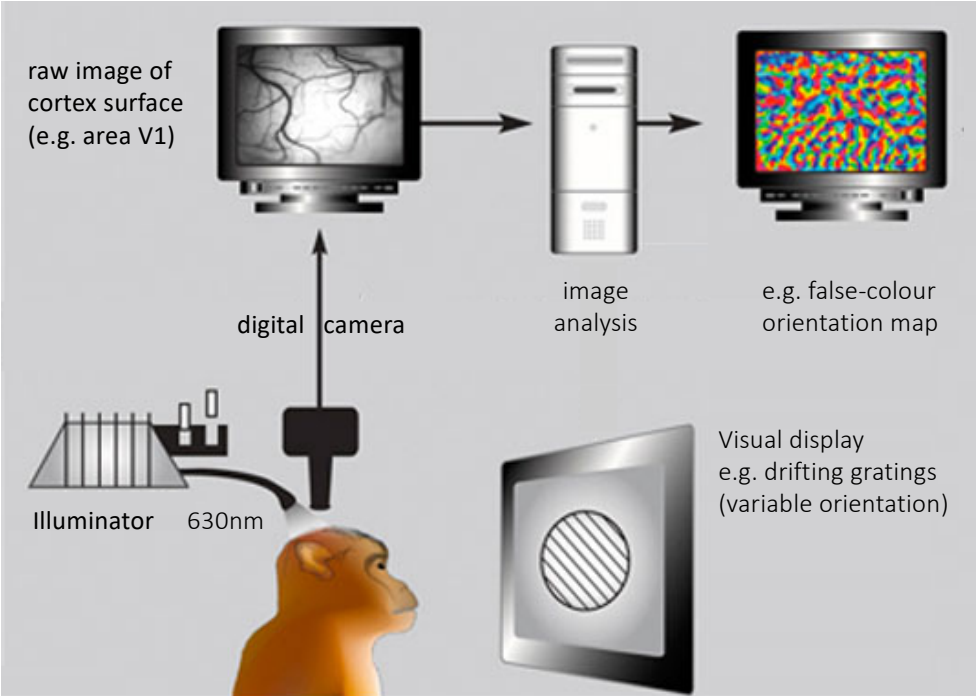
Von der Heydt & Peterhans (1989) [ref. 2]

responses to illusory contours



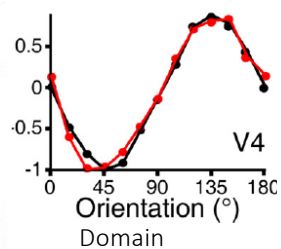
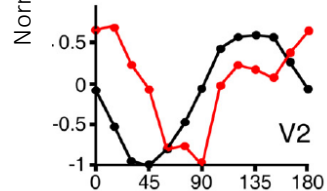
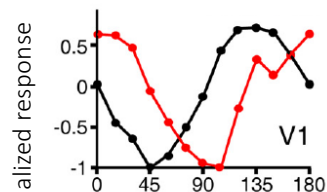
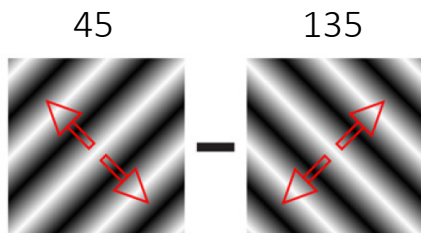
Recordings in area V2

Pan et al (2012) Optical imaging of illusory contour responses: V1, V2 & V4 [\[ref 3\]](#)

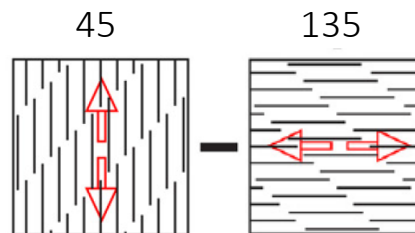


Pan et al (2012) Optical imaging of illusory contour responses: V1, V2 & V4 [ref 3]

luminance grating stimulus



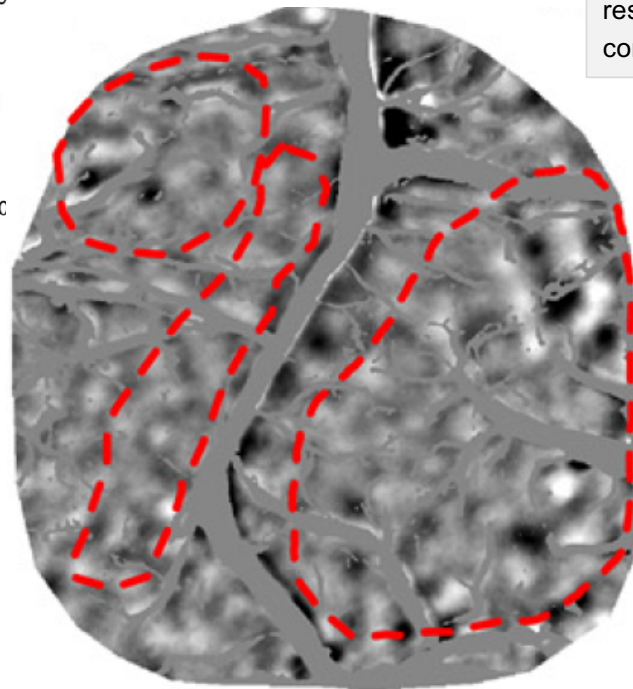
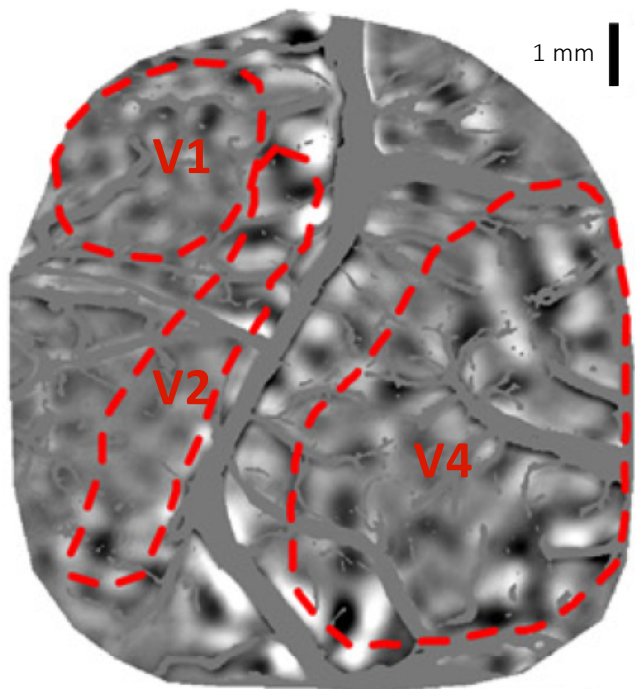
illusory contour stimulus



Optical imaging of the superficial layers of cortex across area V1, V2 and V4 reveals differences in these areas' population responses:

Orientation-tuned mechanisms in V1 and V2 respond preferentially to local contours (i.e. the short vertical and horizontal lines in the illusory contour stimulus);

Orientation-tuned mechanisms in V4 respond preferentially to the global, illusory contours in the illusory contour stimulus.

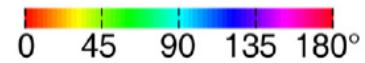
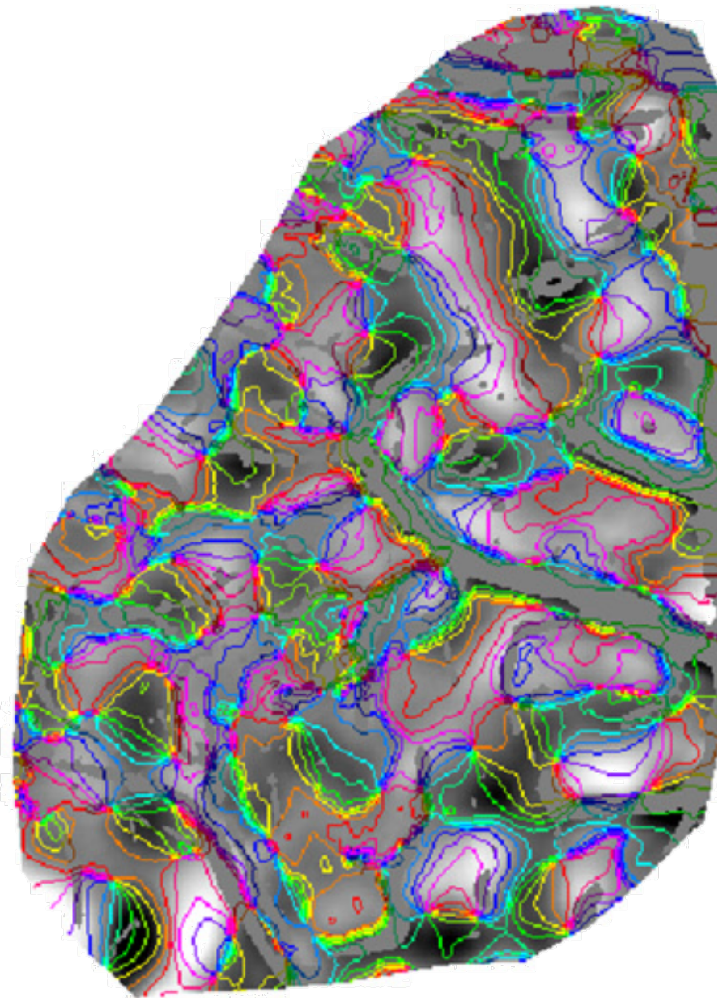
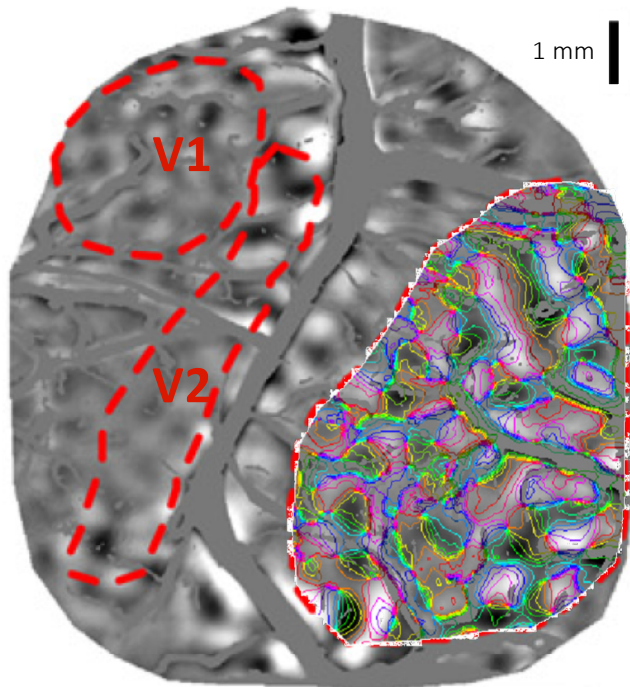
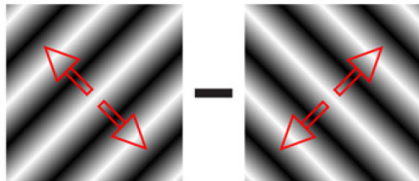


Pan et al (2012) Optical imaging of illusory contour responses: V1, V2 & V4 ^[ref 3]

luminance grating

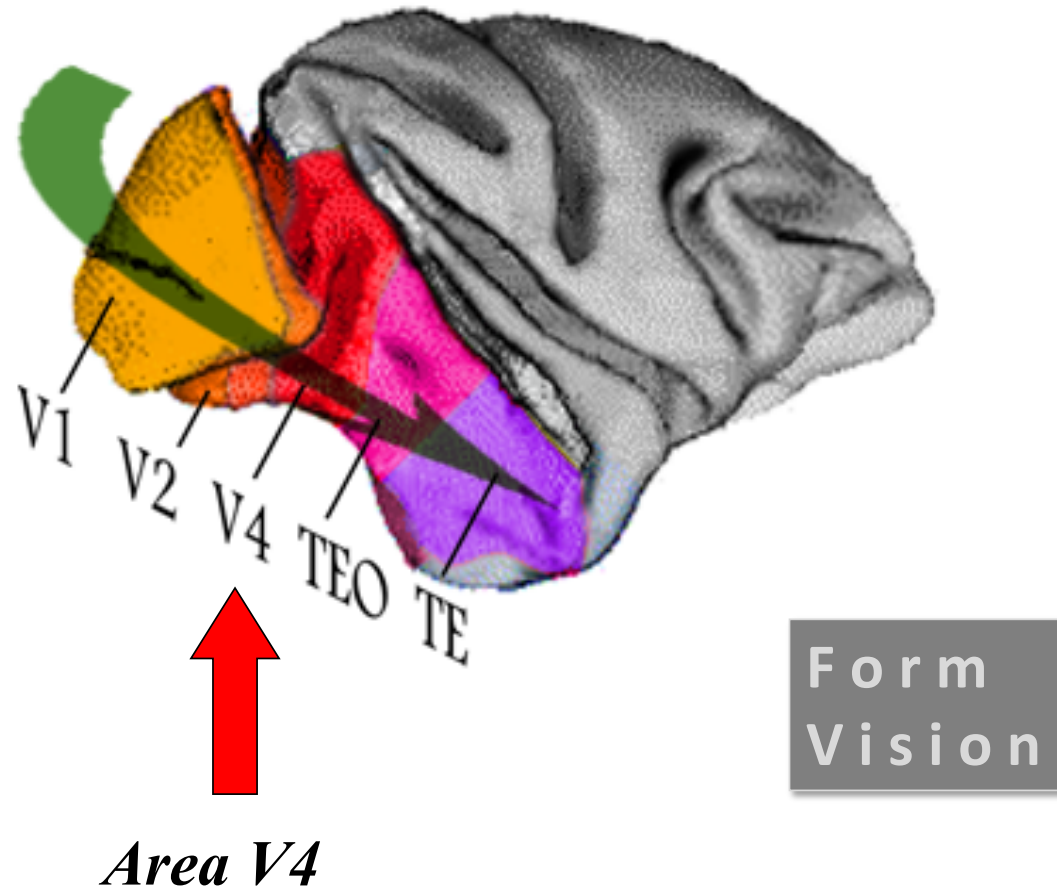
45

135



Orientation map of V4:
orientation domains at 30°
intervals

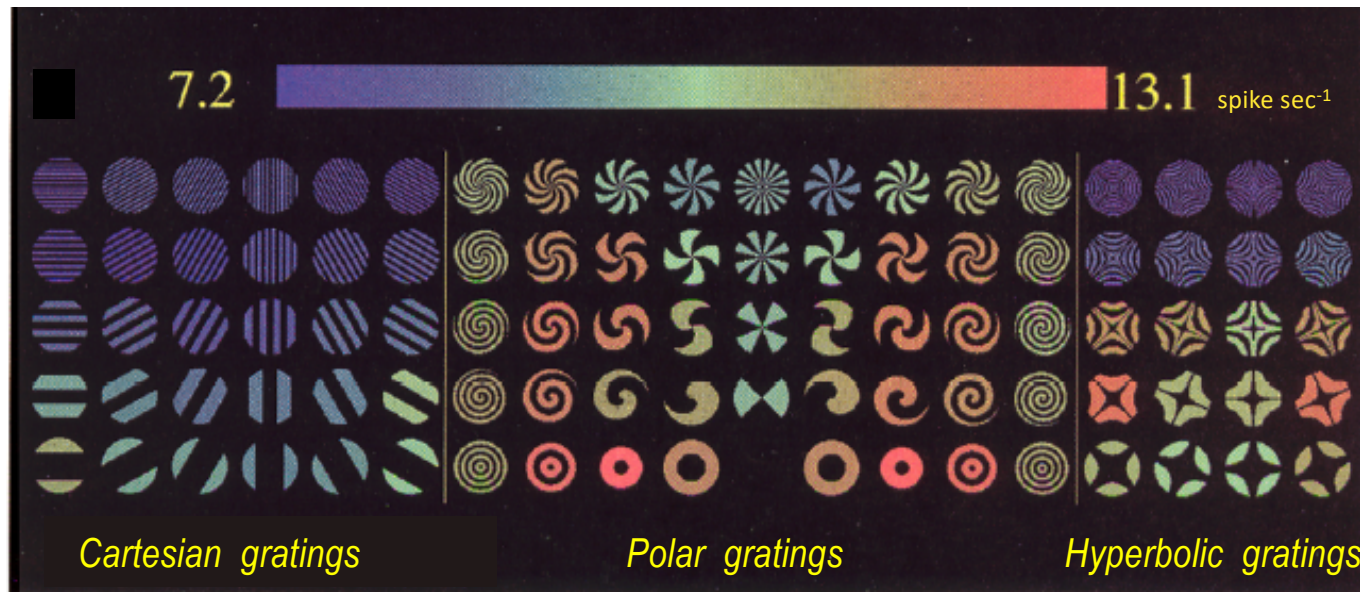
The ventral visual pathway...



Gallant *et al.* (1996) [ref 5]

V4 neurons tested with Cartesian, polar and hyperbolic gratings

Neural response is coded by the blue-red 'heat' scale.



The average response (across the sampled population of V4 neurons) to both forms of curved gratings was far greater than the response to linear gratings.

CONCLUSION: V4 shows the development of selectivity for curvature.

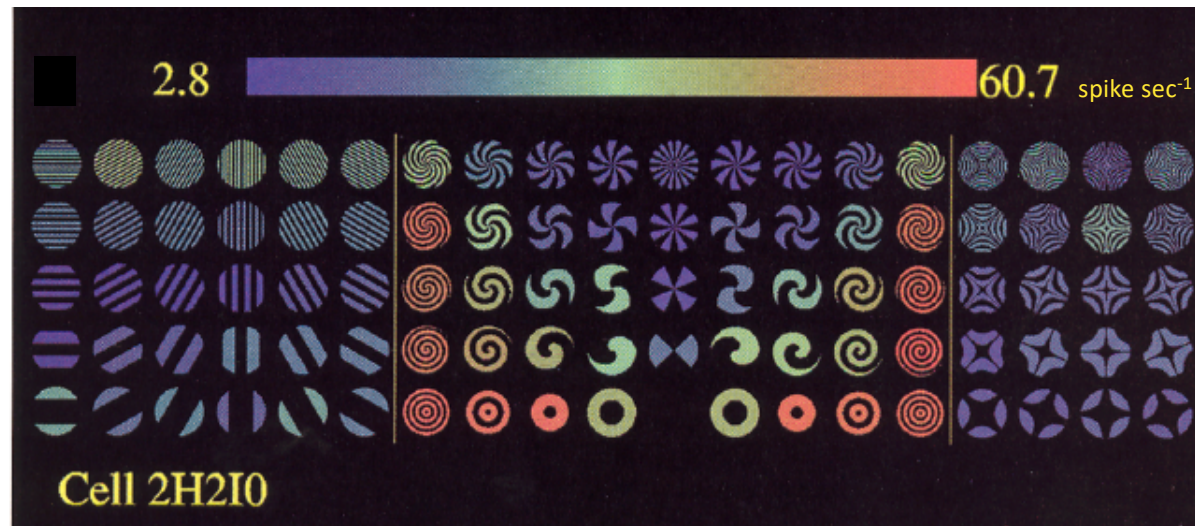
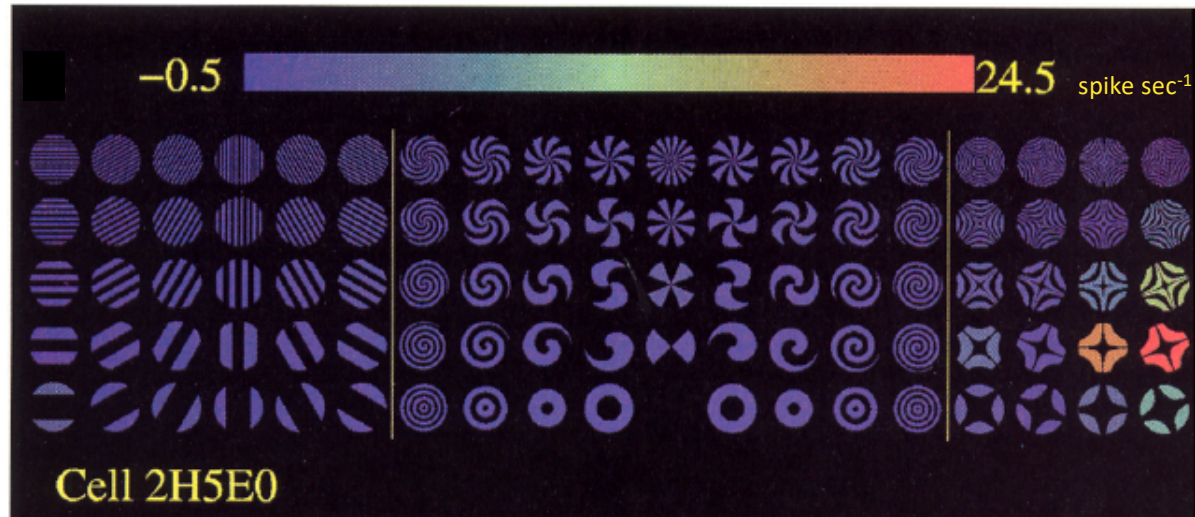
Gallant *et al.* (1996) [ref 5]

V4 neurons tested with Cartesian, polar and hyperbolic gratings

Some cells were highly selective within this stimulus space...

The response of the neuron is coded by the blue-red 'heat' scale.

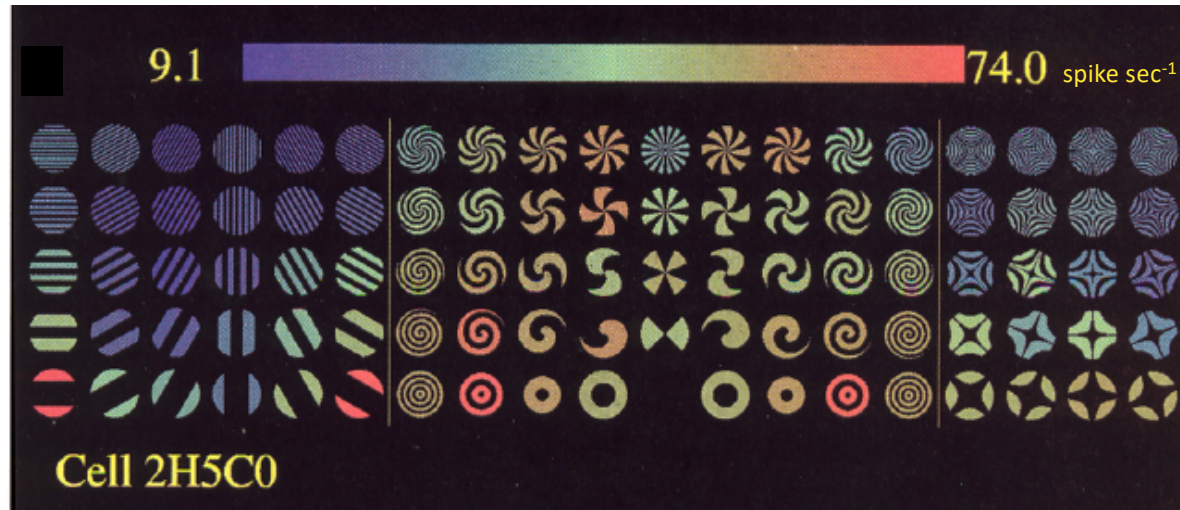
Cell '2H5E0' was selectively responsive to hyperbolic gratings only;



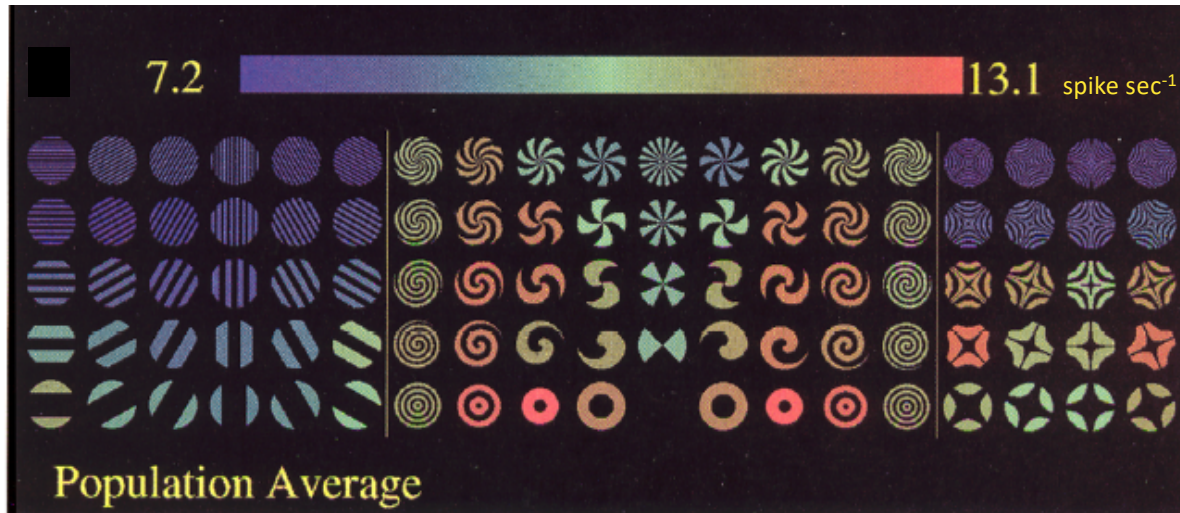
Cell '2H2I0' was selective for cartesian gratings.

Gallant *et al.* (1996) [ref 5]

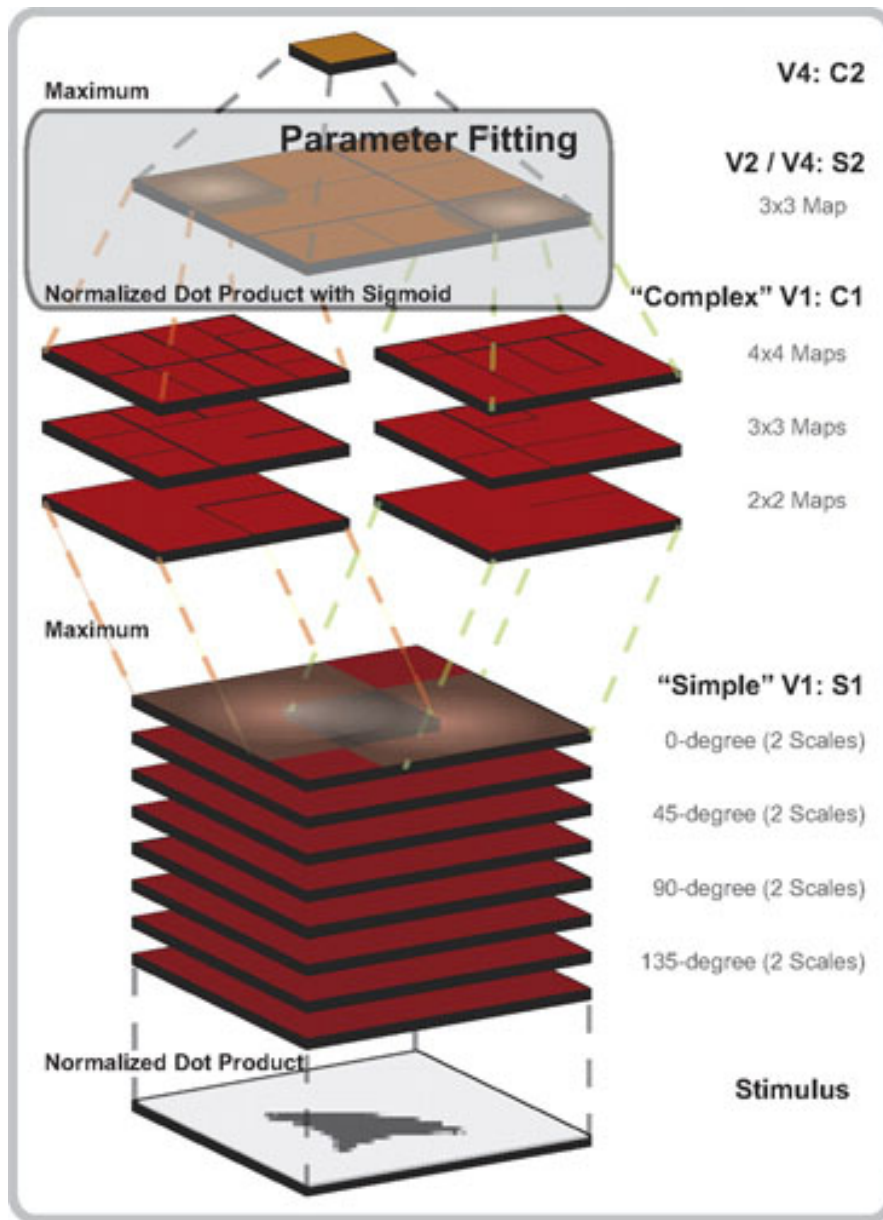
V4 neurons tested with Cartesian, polar and hyperbolic gratings



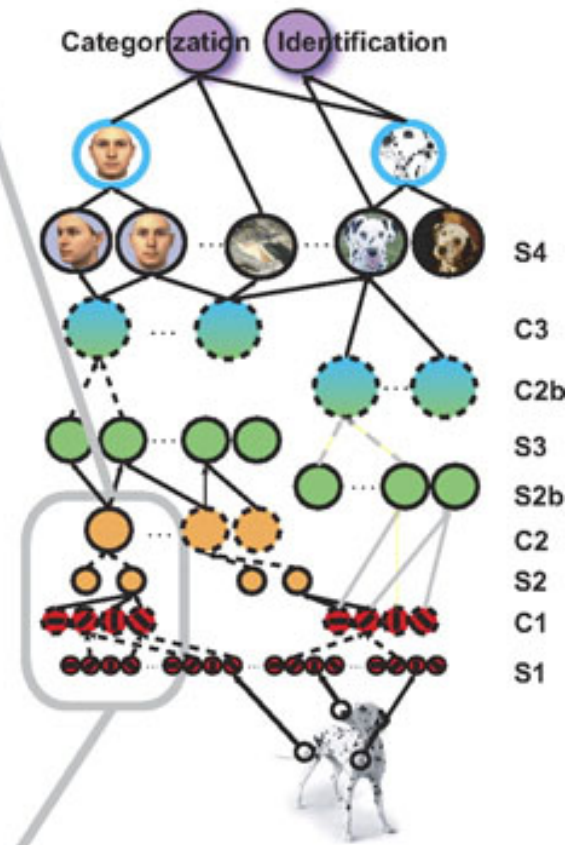
...other neurons were less selective.



The average response to both forms of curved gratings was greater than the response to linear gratings.



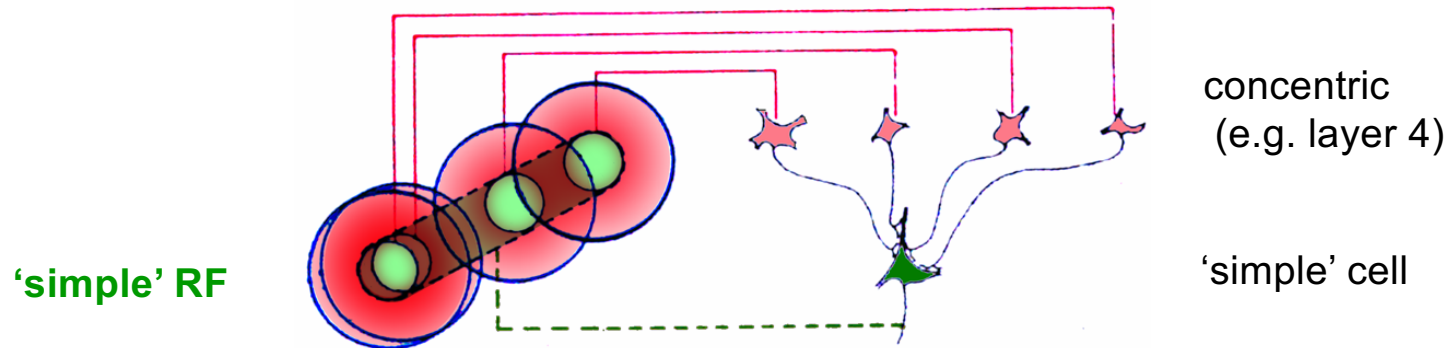
Model of object recognition within full ventral visual pathway
Cadiou, Poggio *et al* (2007) [ref 9]



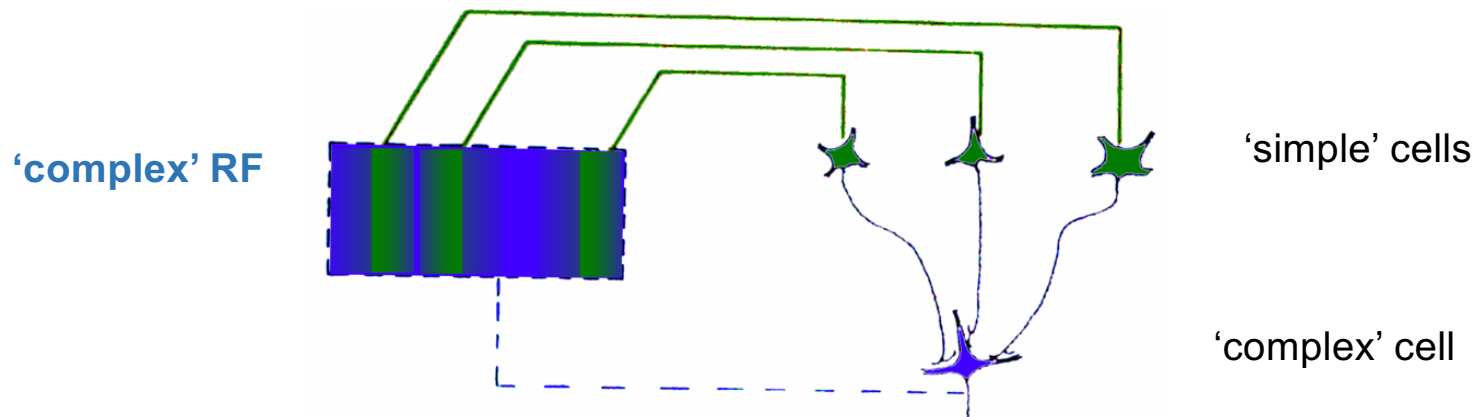
- But models solely forward connections, not backward connections !

○	Simple cells	—	Main routes
⊙	Complex cells	- -	Bypass routes
—	Tuning		
- -	Softmax		

Hubel & Wiesel: hypothesis for construction of 'simple' and 'complex' receptive fields



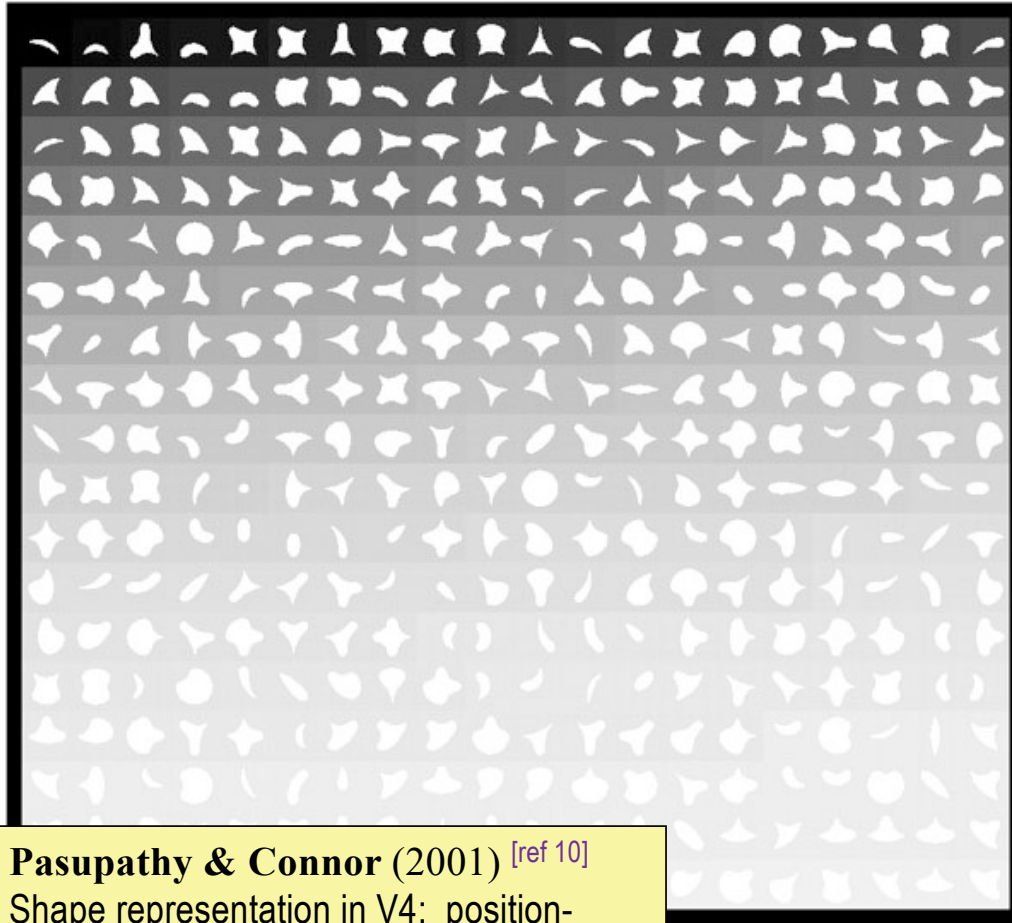
Cadieu, Poggio: 'Selectivity' operation creates specificity of response = Logical 'AND'



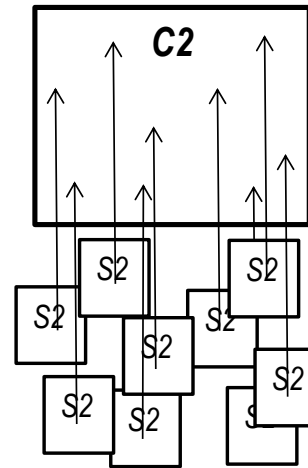
Cadieu, Poggio: 'Max' operation creates invariance of response = Logical 'OR'

Model of object recognition within
full ventral visual pathway
Cadieu *et al* (2007) [ref 9]

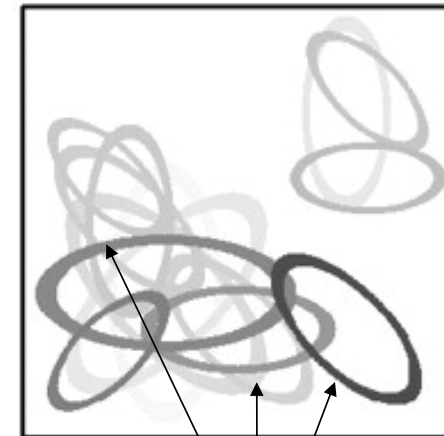
Model response of C2 neuron



Pasupathy & Connor (2001) [ref 10]
Shape representation in V4: position-
specific tuning for boundary conformation.

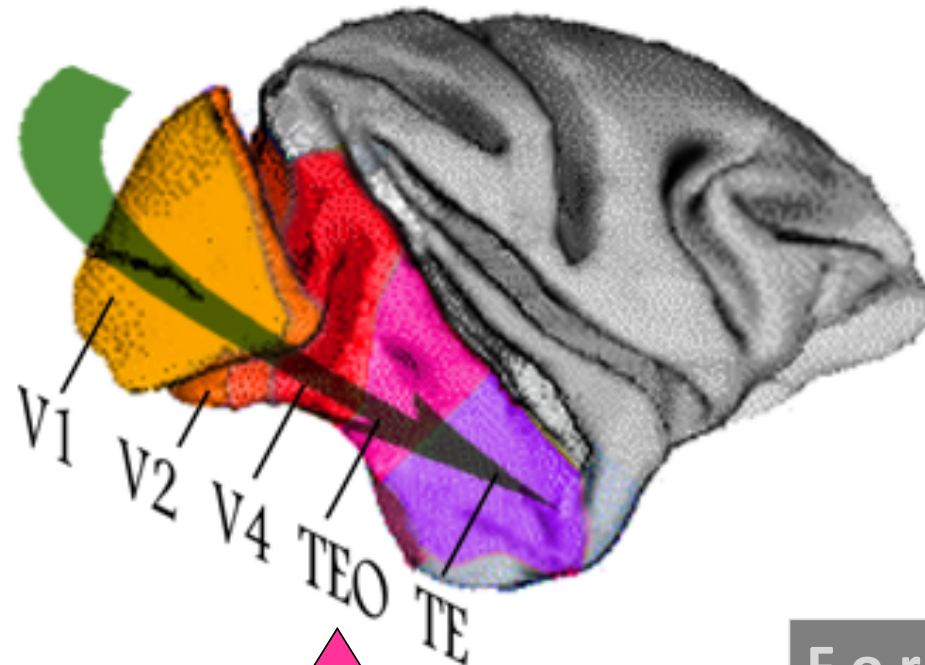


Model of 'S2' neuron



Pooled 'C1' inputs

The ventral visual pathway...



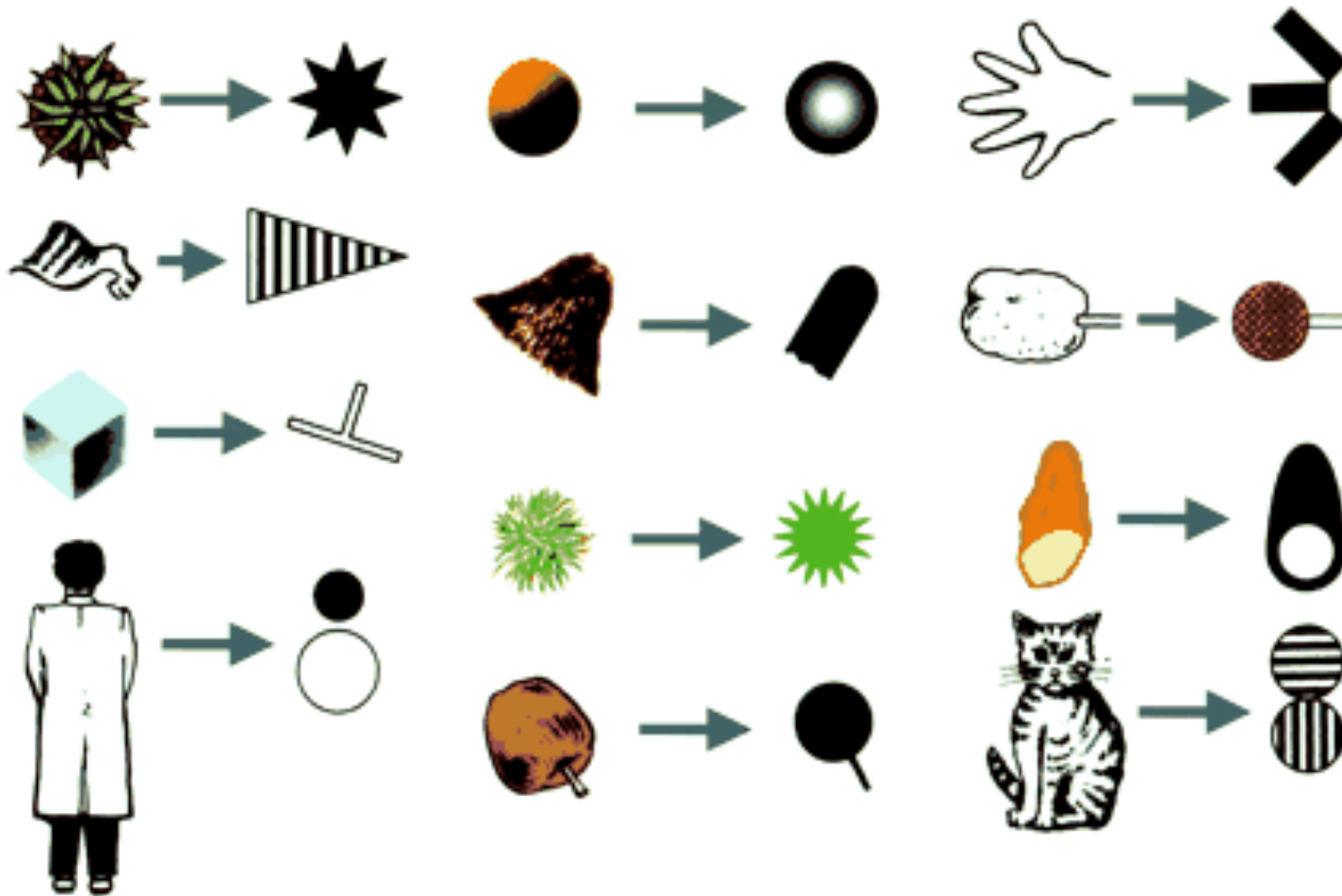
Form
Vision

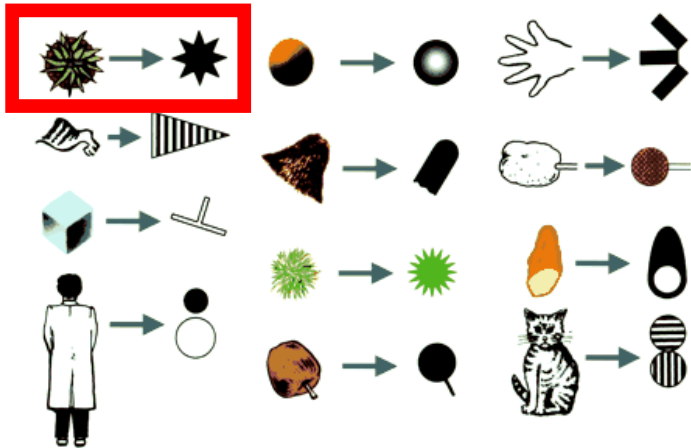
↑ ↑
Areas TEO & TE

- known together as 'IT cortex' (inferior temporal)

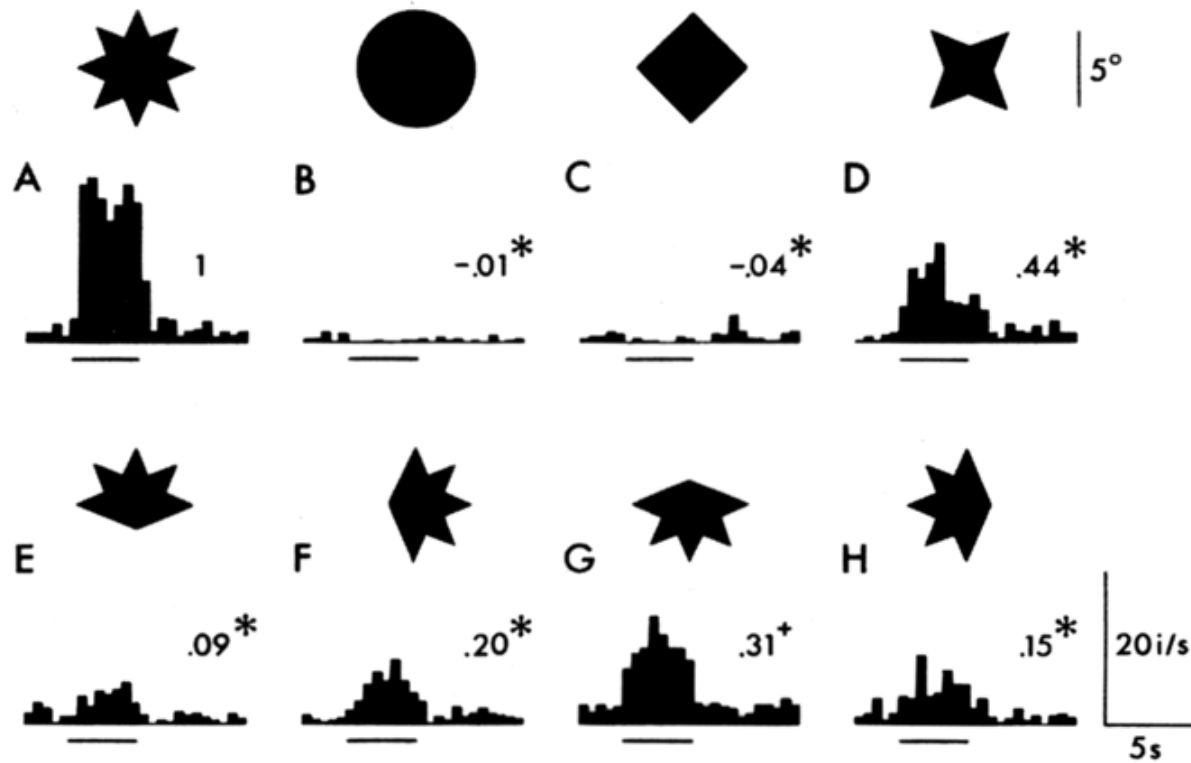
Tanaka *et al* (1991/2003) [ref. 6] *complex object sensitivity of IT cells*

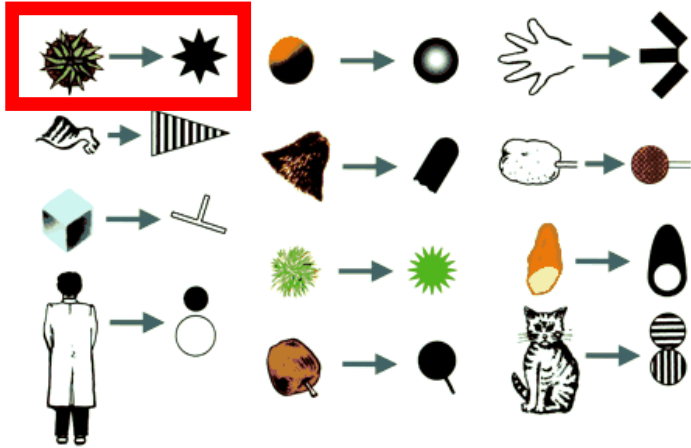
The 'image reduction' method





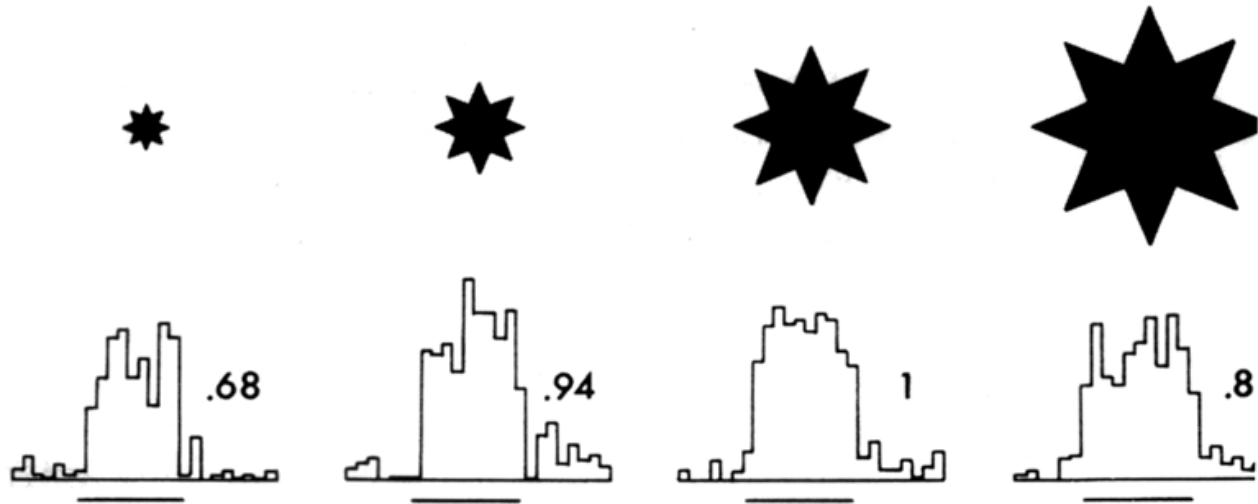
Tanaka *et al* (1991) [ref.6]
complex object sensitivity of IT cells

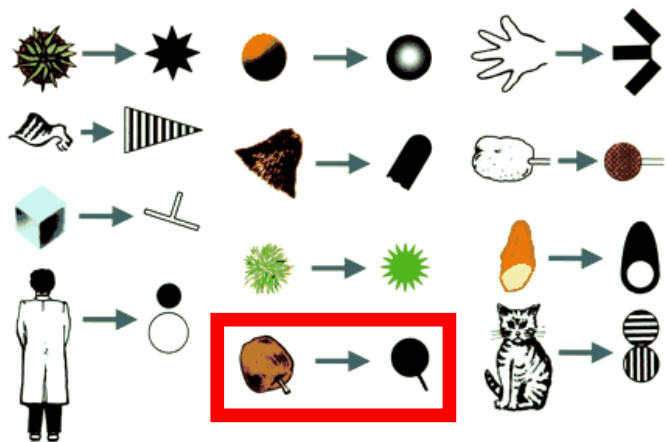




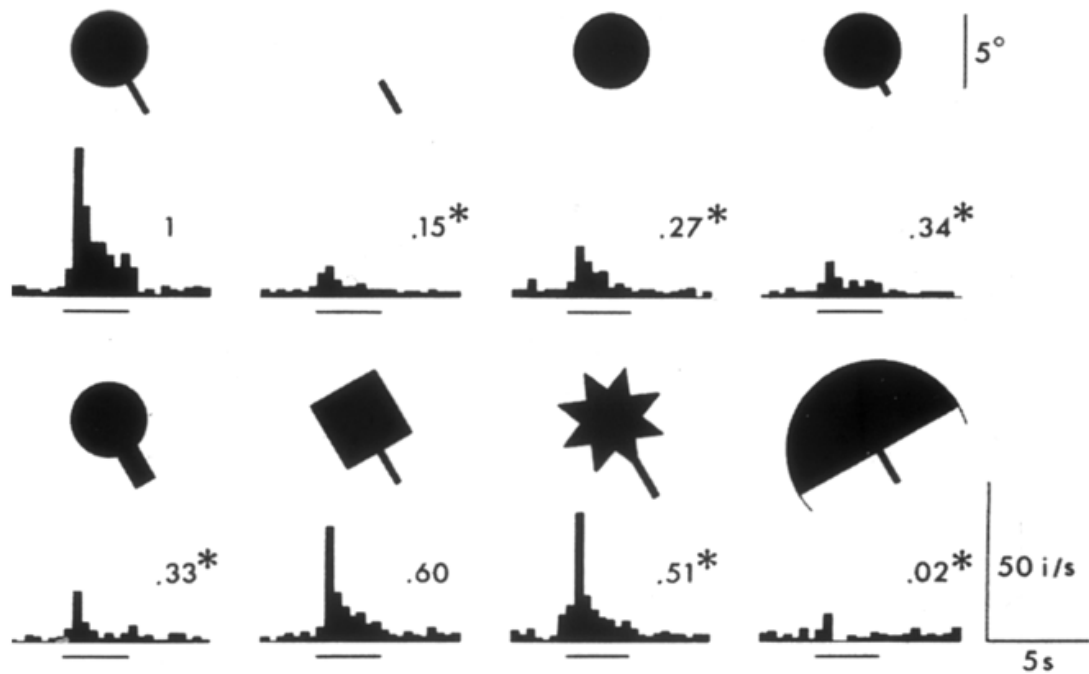
Tanaka *et al* (1991) [ref.6]
complex object sensitivity of IT cells

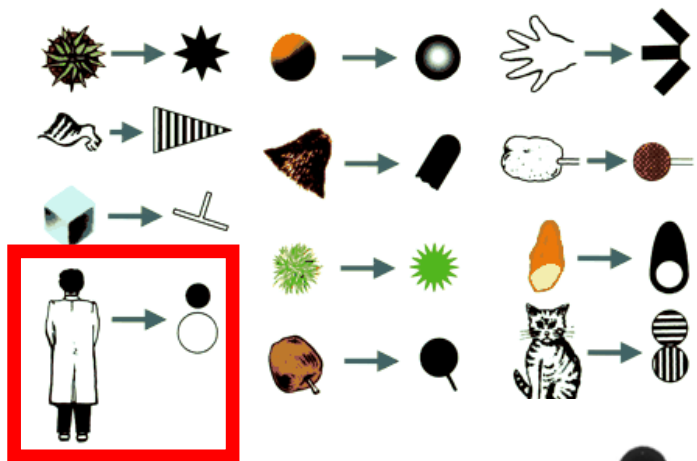
'size invariance'



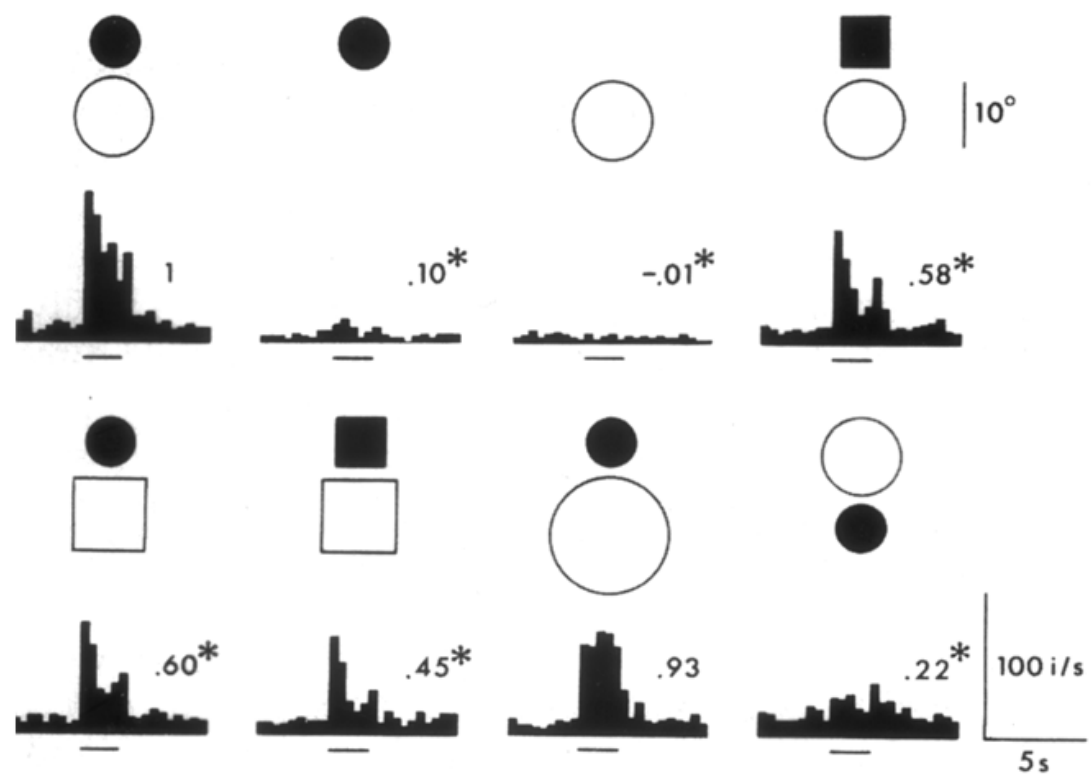


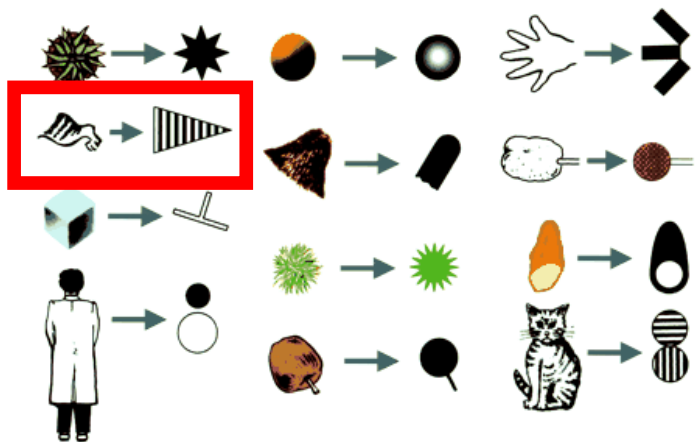
Tanaka *et al* (1991) [ref.6]
complex object sensitivity of IT cells



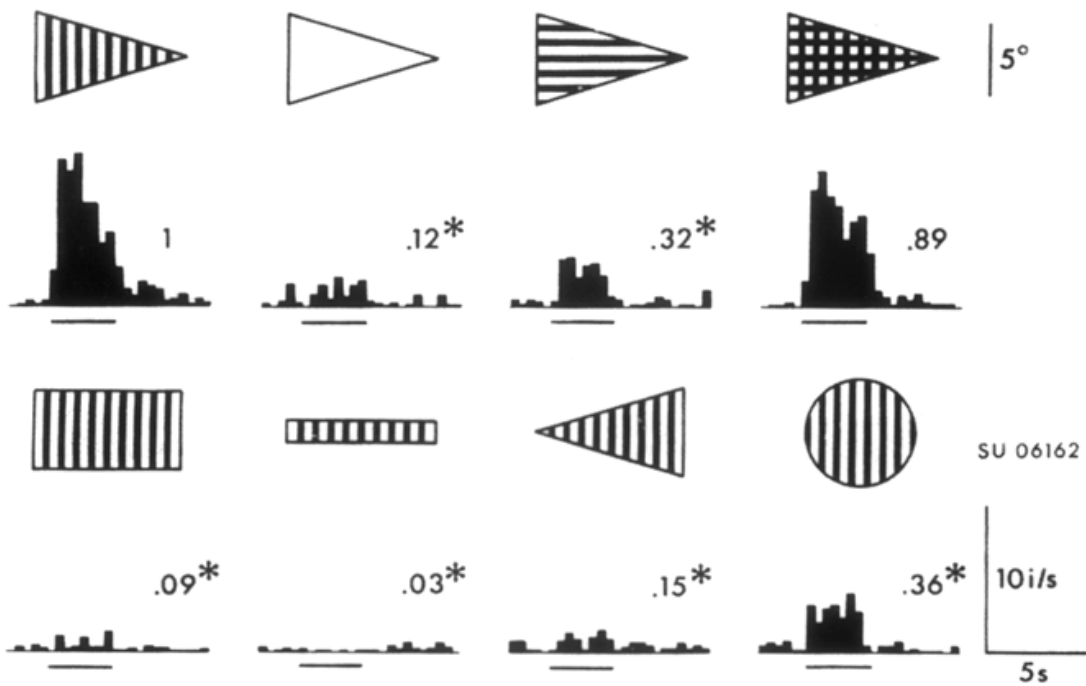


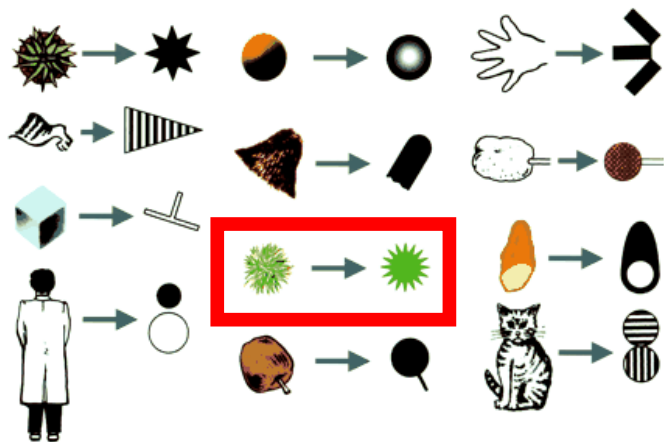
Tanaka *et al* (1991) [ref.6]
complex object sensitivity of IT cells





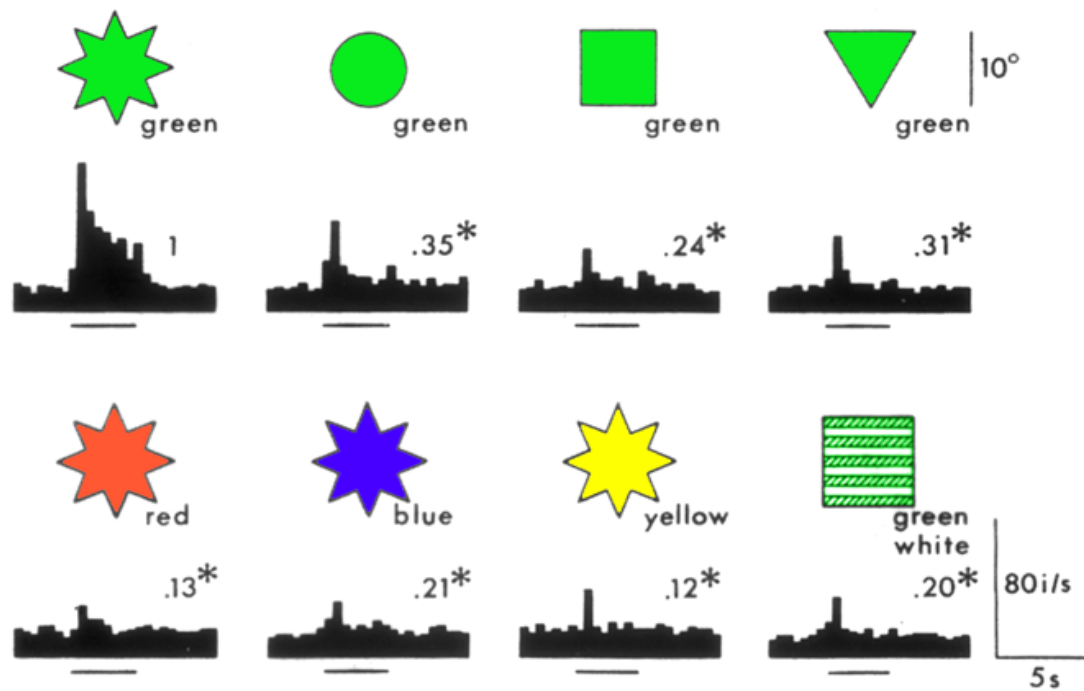
Tanaka *et al* (1991) [ref.6]
complex object sensitivity of IT cells





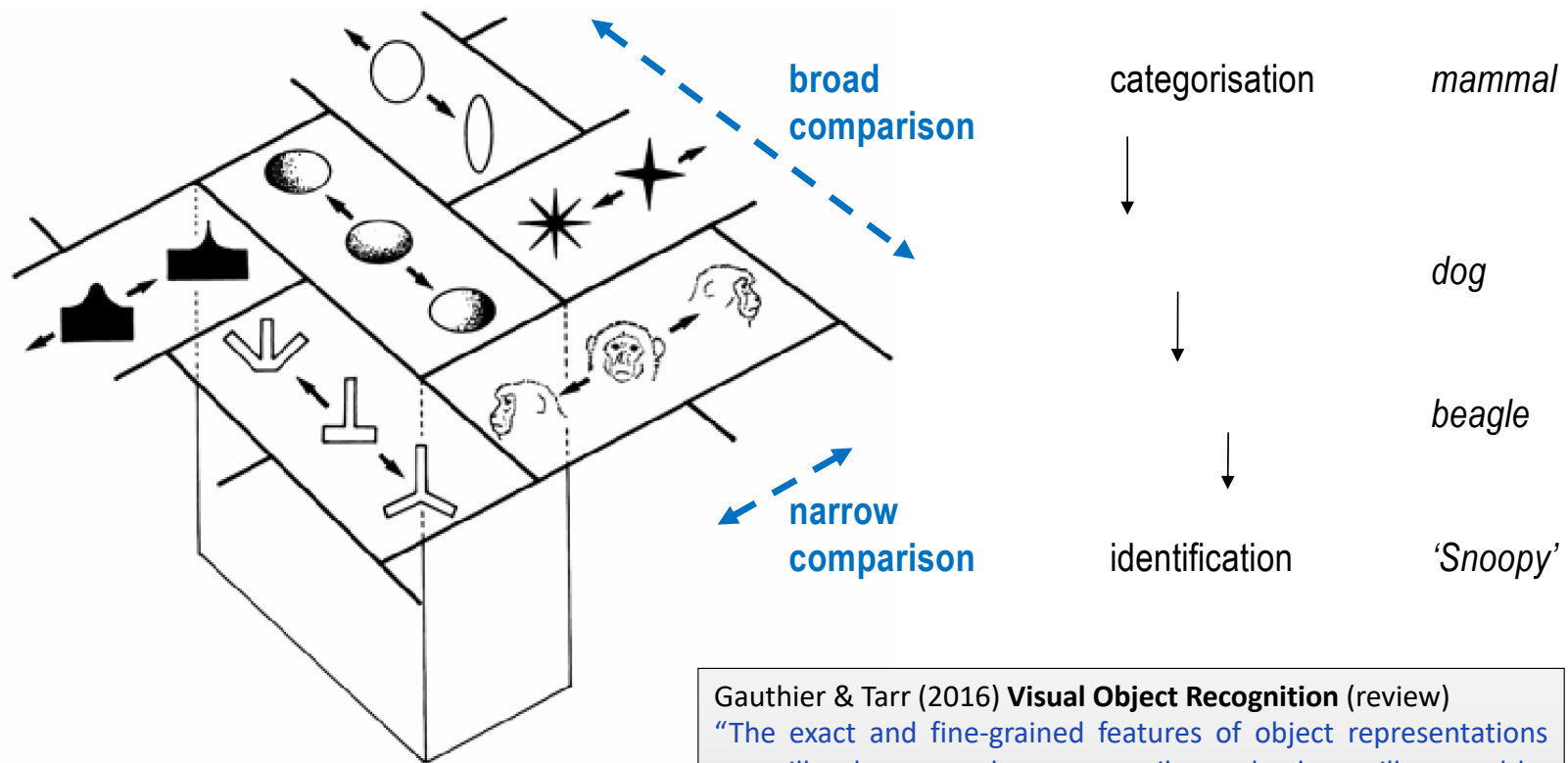
Tanaka *et al* (1991) [ref.6]
complex object sensitivity of IT cells

*combination of colour
 & form selectivity*



What is the neural basis of object recognition...?

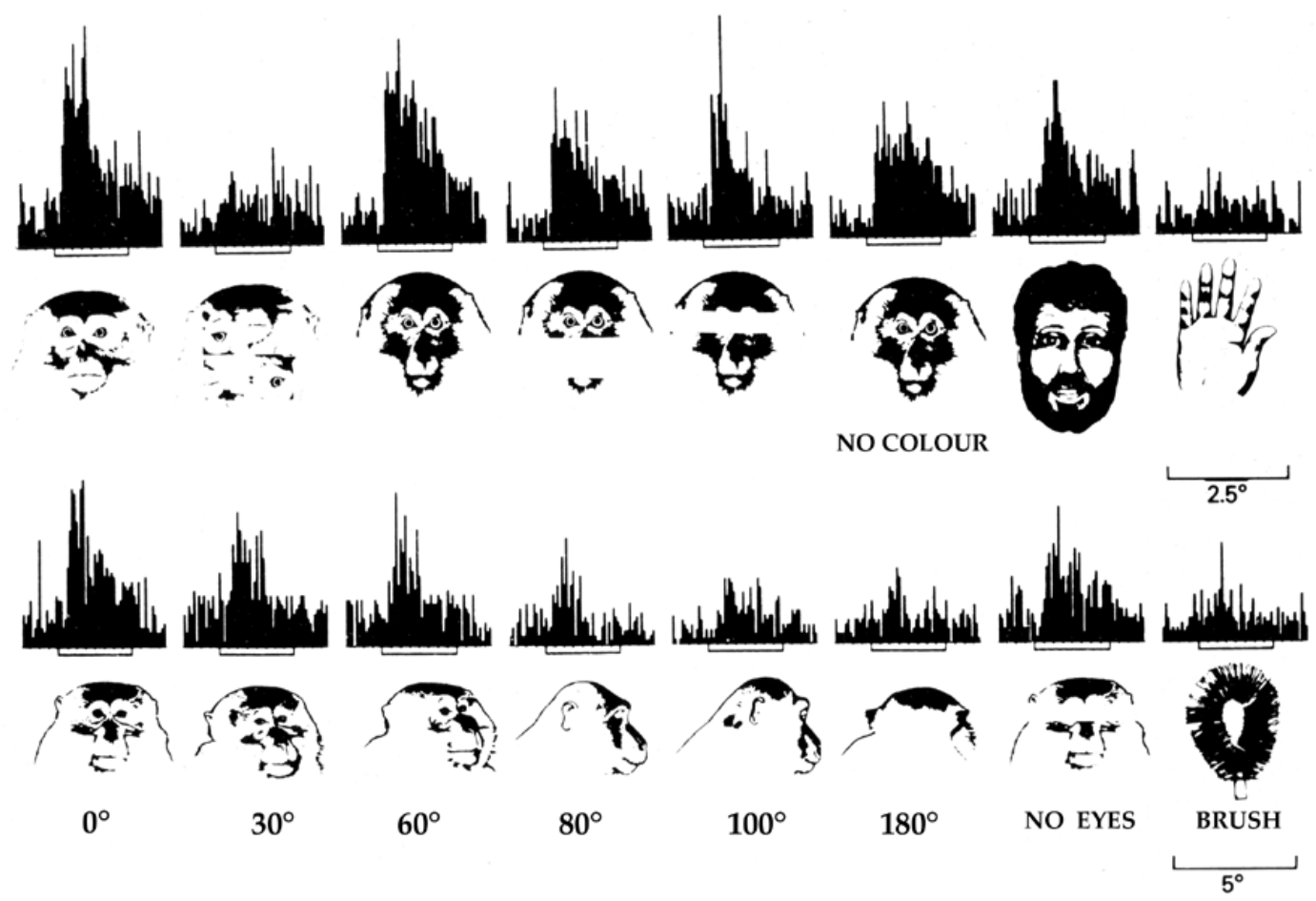
Tanaka *distributed code for object representation*
(as opposed to 'Grandmother' cells)



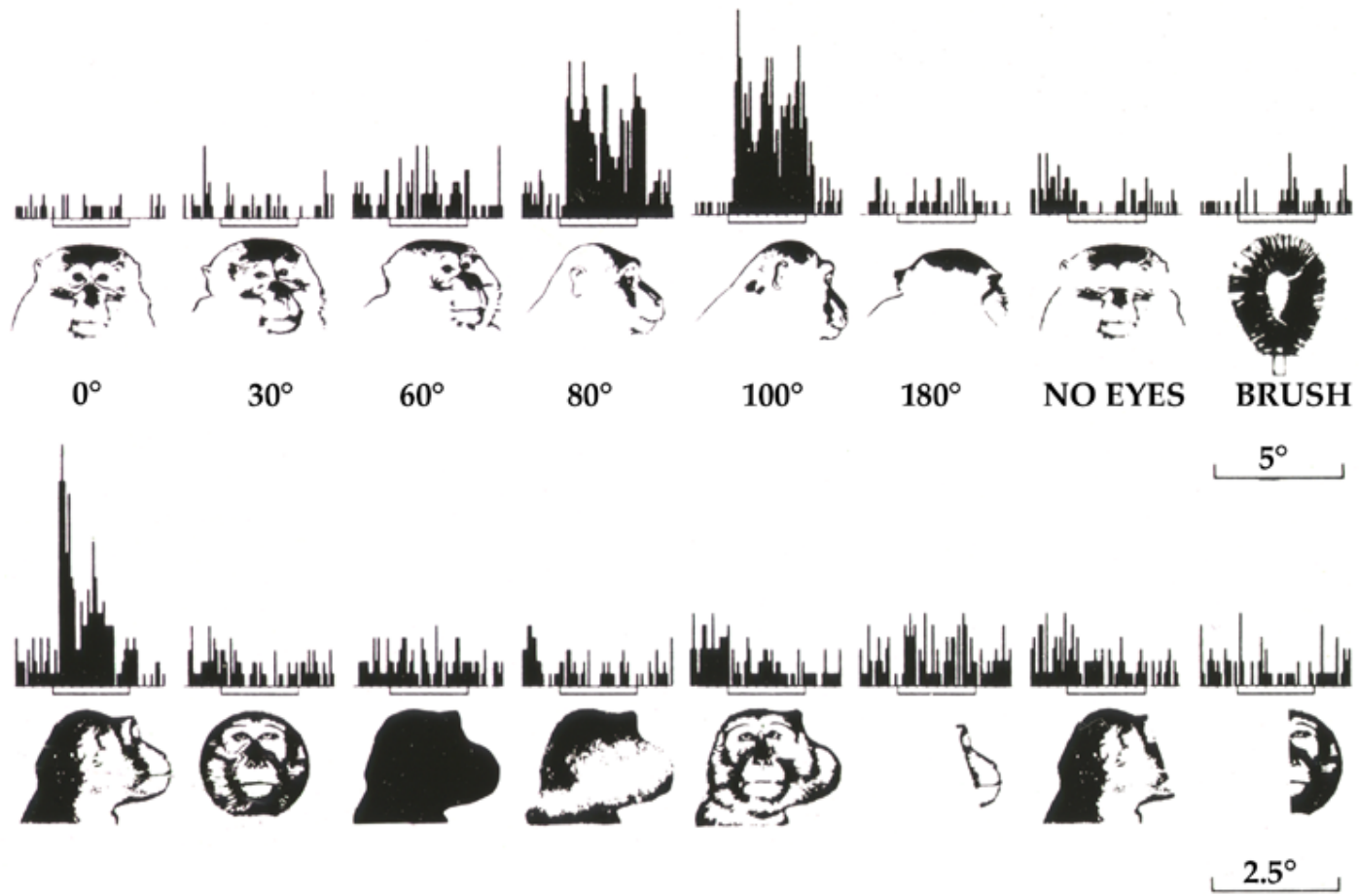
Tanaka's model of IT cortex
- nearby columns have similar properties

Gauthier & Tarr (2016) **Visual Object Recognition** (review)
"The exact and fine-grained features of object representations are still unknown and are not easily resolved – as illustrated by our failure as a field to come up with a comprehensive model of the recognition process"

Desimone et al 1984 [ref. 8] *STS cells sensitive to face stimuli*

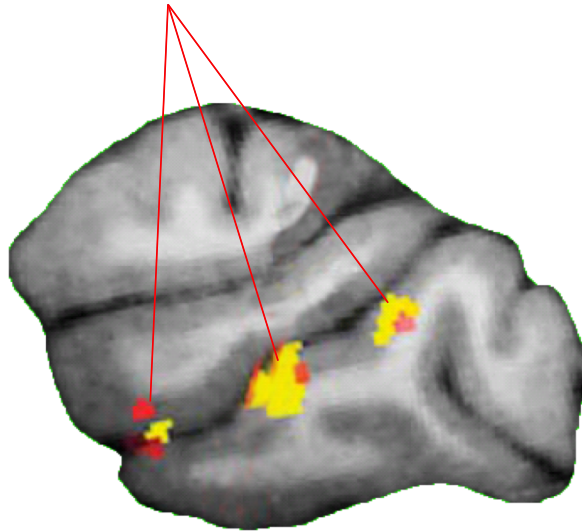


Desimone et al 1984 [ref. 8] *STS cells sensitive to face stimuli*

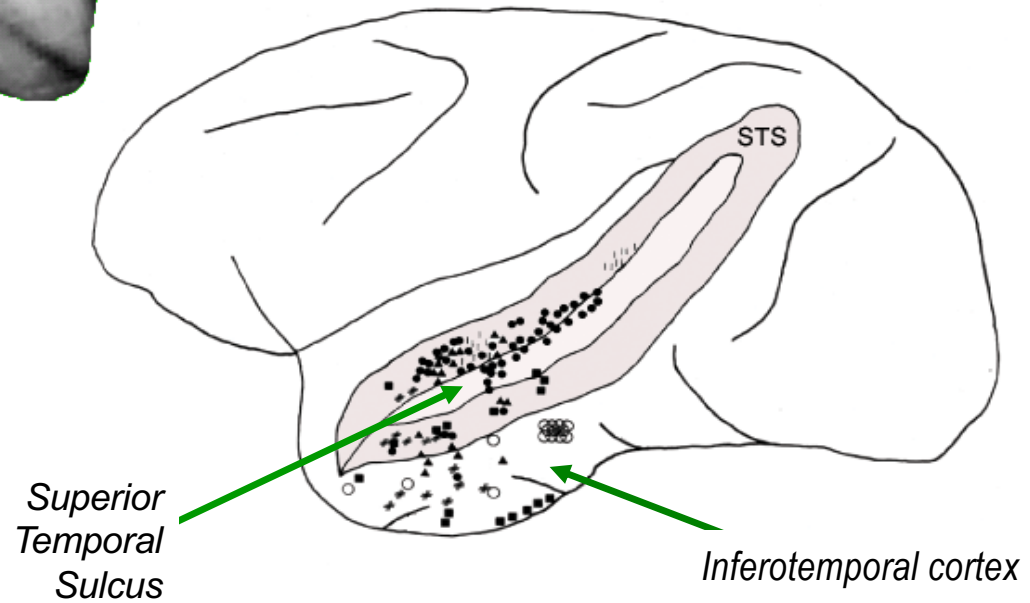


Tsao et al (2006) *Face processing centres in STS observed by fMRI*

'face patches' revealed by fMRI

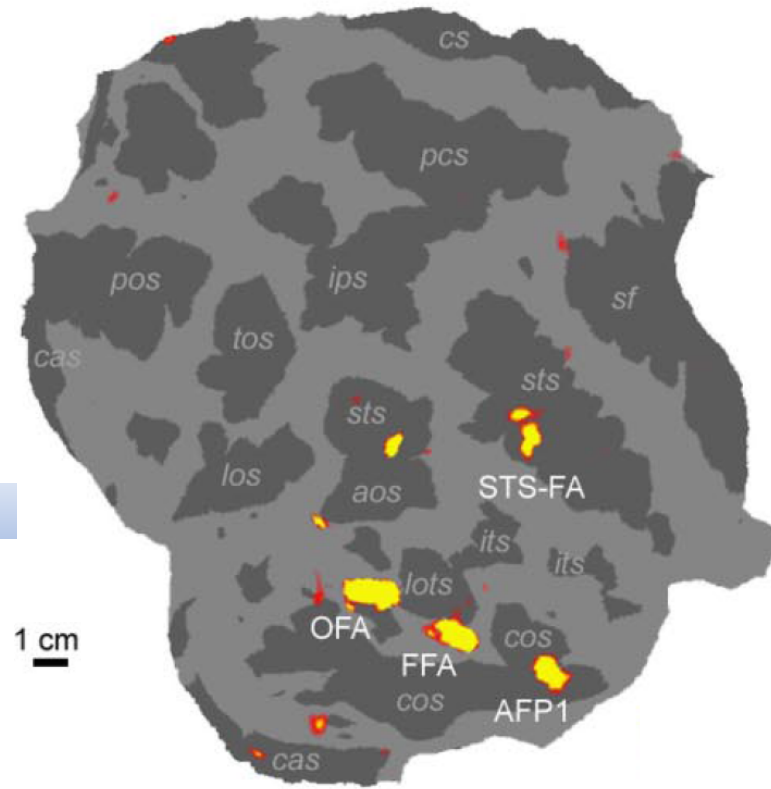
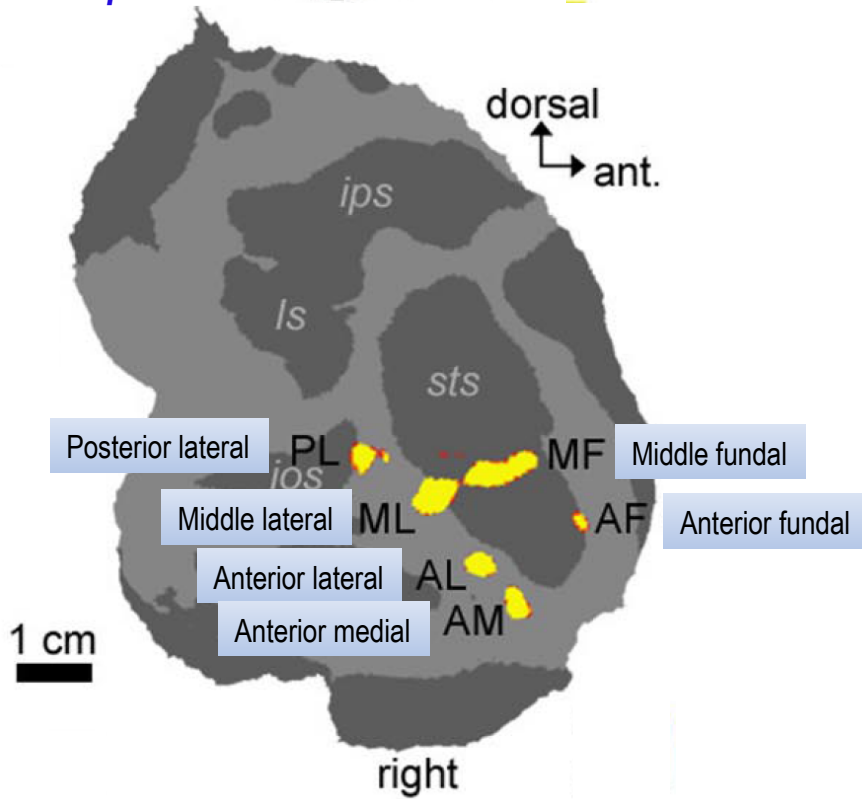
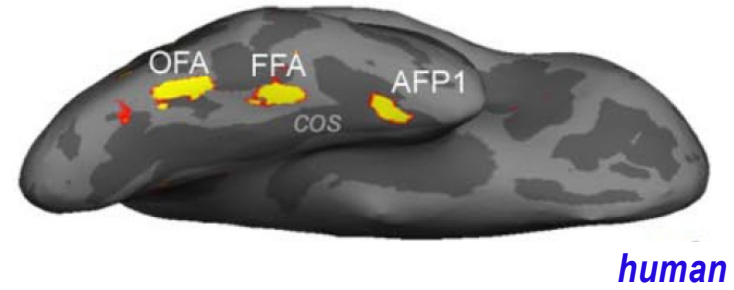
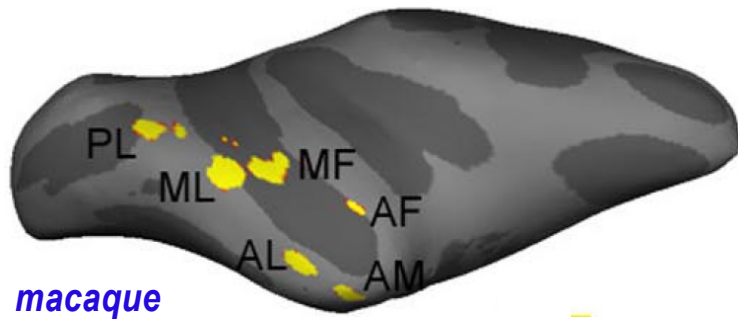


Collation of face sensitive cell sites
c. 1992



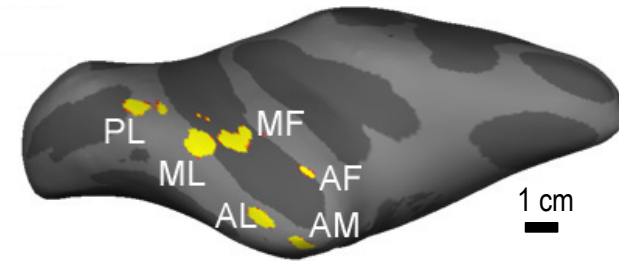
Tsao *et al* (2008) [ref 12]

Comparing face patch systems in macaques & humans



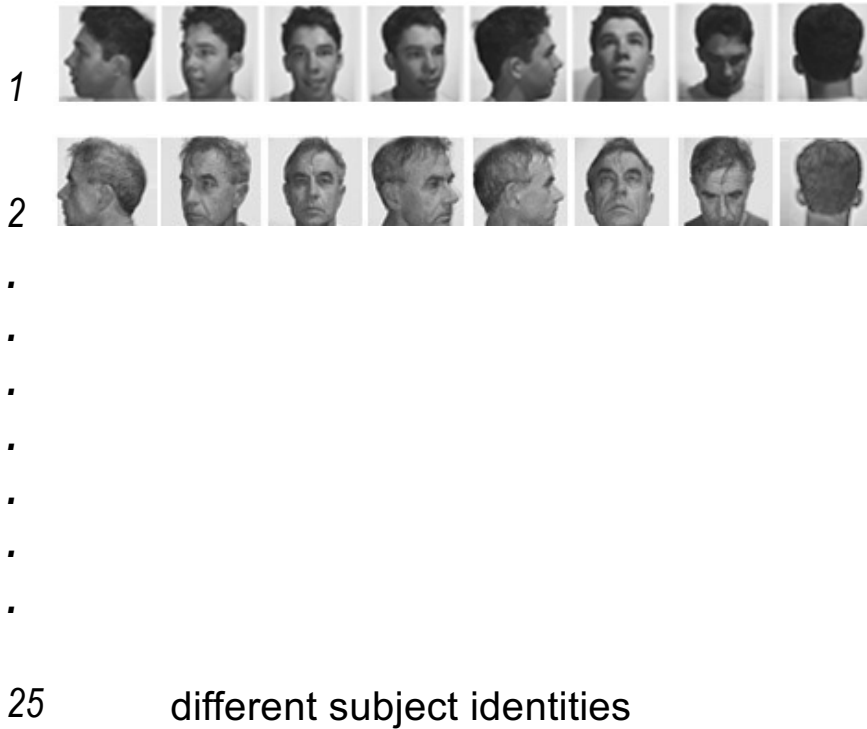
Freiwald & Tsao (2010) [ref 13]

Face neurons: (a) view selectivity & view invariance;
(b) individual face selectivity.

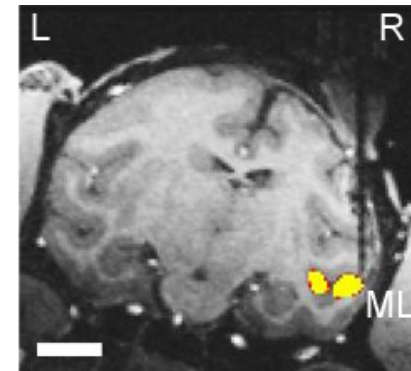


Stimuli

8 face view angles



Neurophysiology

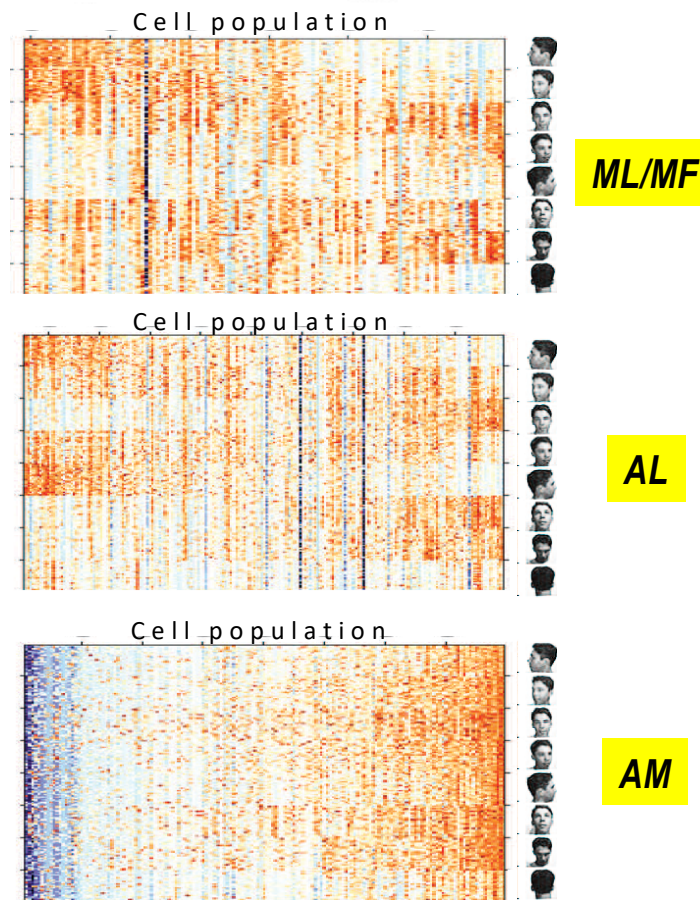
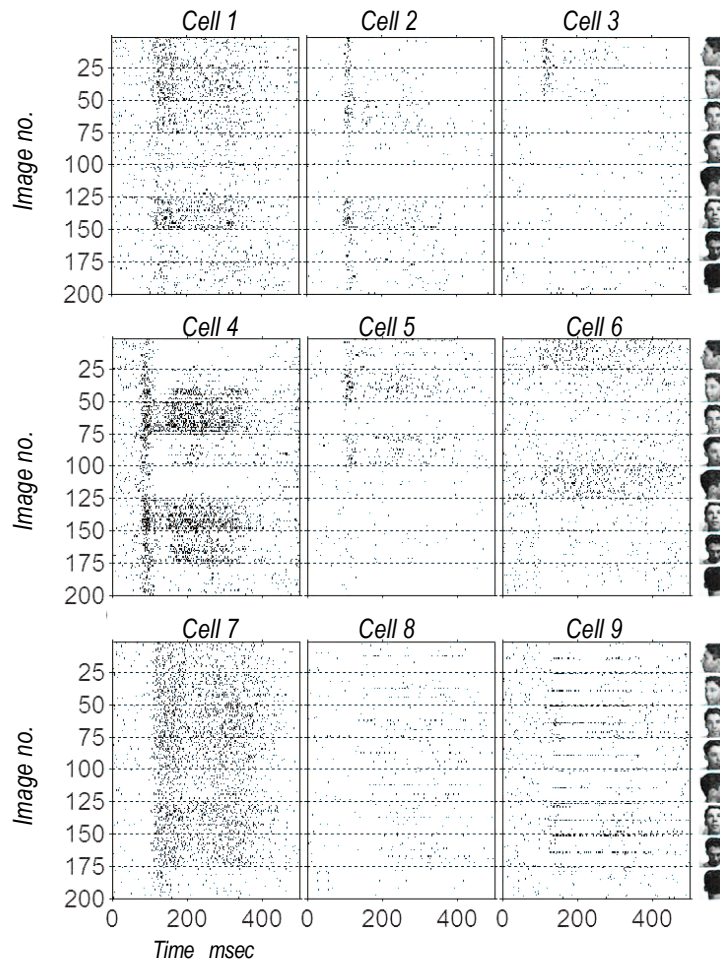
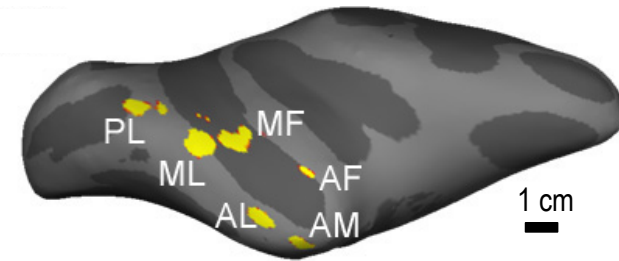


Recordings in 4 patches:

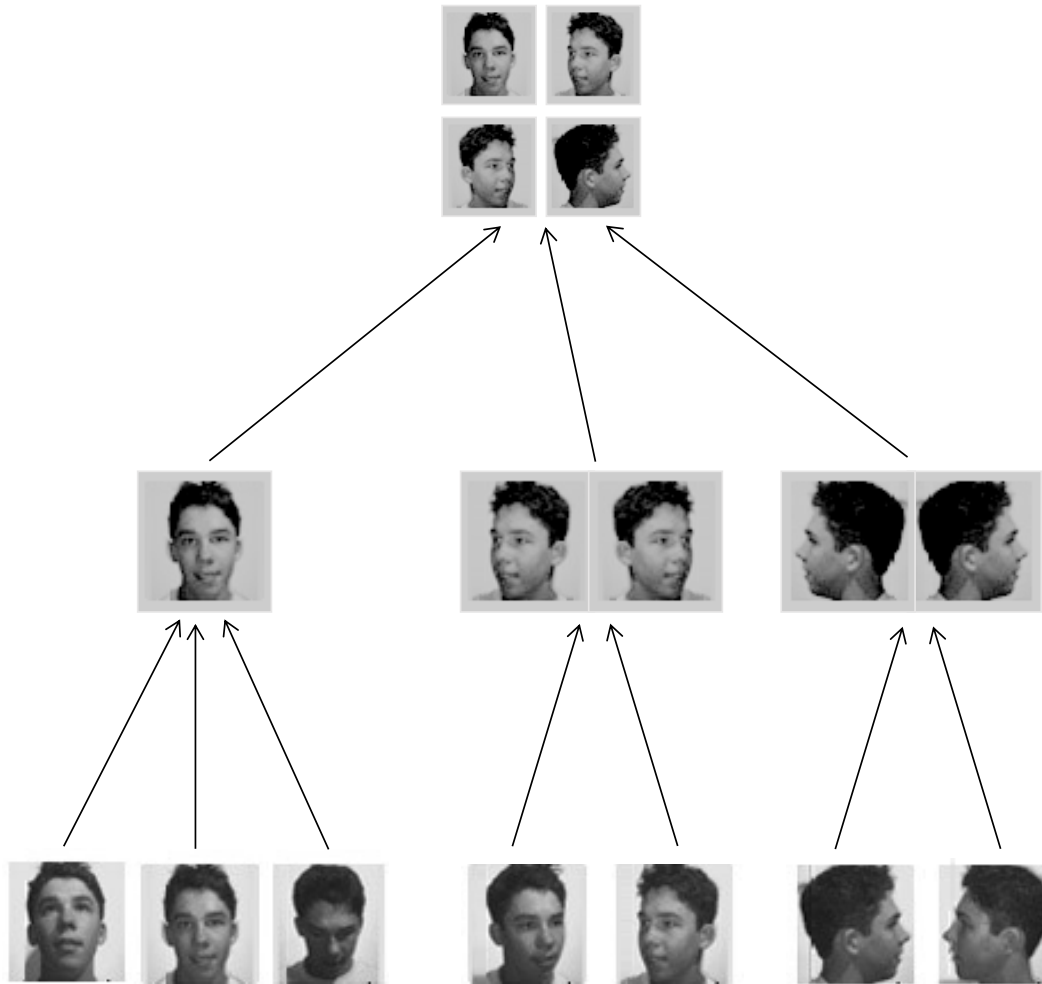
- ML & MF**
- AL**
- AM**

Friewald & Tsao (2010) [ref 13]

Face neurons: (a) view selectivity & view invariance;
(b) individual face selectivity.



Friewald & Tsao (2010) *[ref 13]*
Hierarchical model



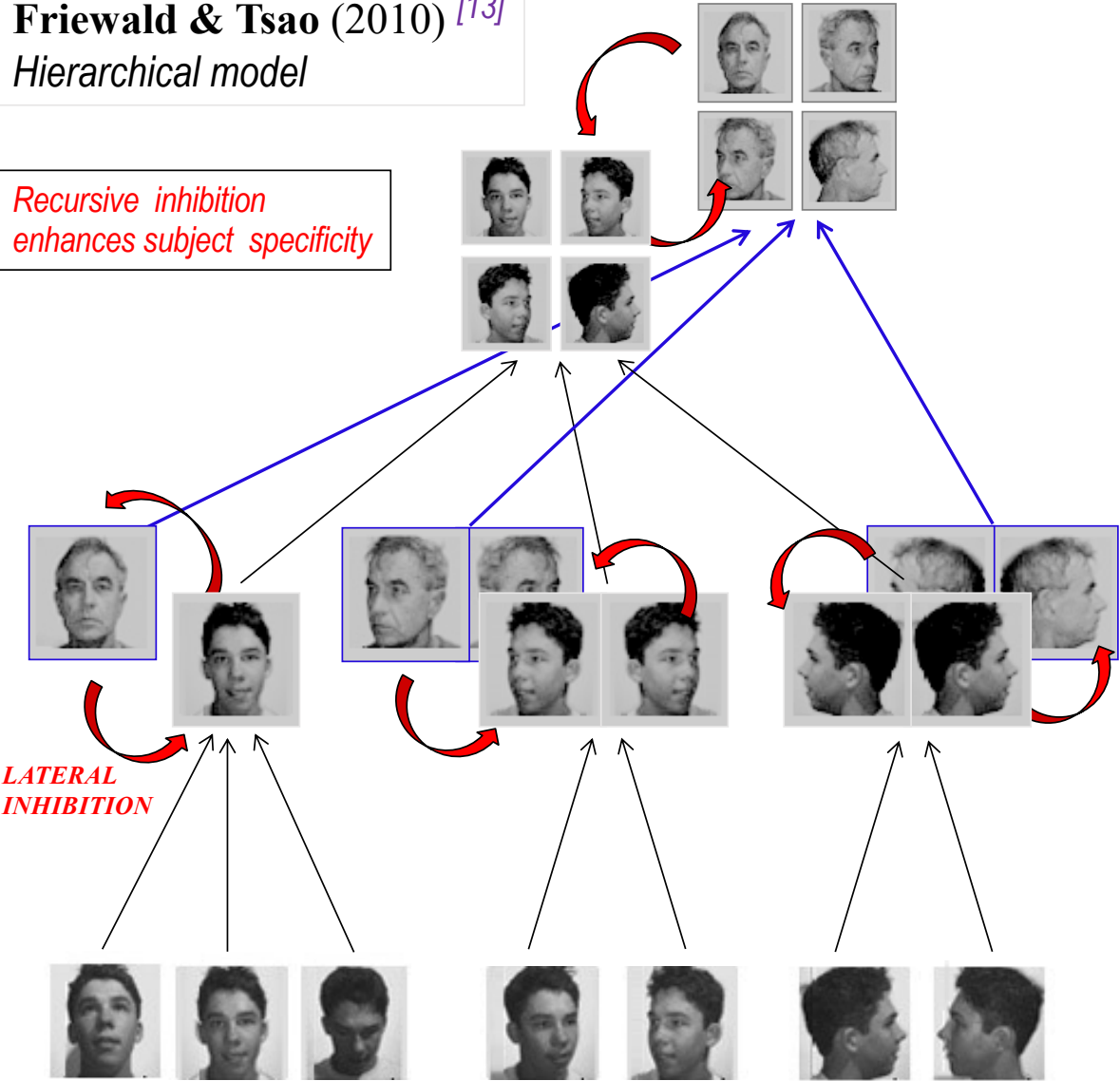
AM patch
'View invariant'
latency = 124 msec

AL patch
'View symmetrical'
latency = 104 msec

ML/MF patches
'View selective'
latency = 88 msec

Friewald & Tsao (2010) [13]
Hierarchical model

*Recursive inhibition
enhances subject specificity*



AM patch
'View invariant'
latency = 124 msec

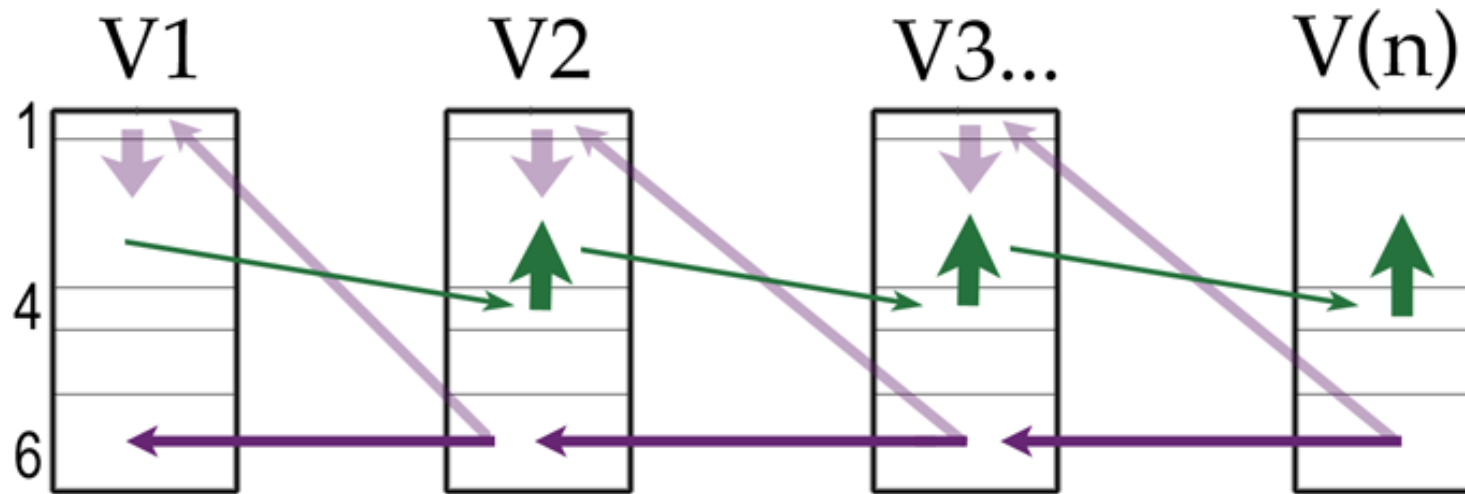
AL patch
'View symmetrical'
latency = 104 msec

ML/MF patches
'View selective'
latency = 88 msec

Visual evidence seeking an explanation...



ascending pathways



*descending pathways
(feedback)*



Visual hypothesis seeking corroborative evidence

Perception as an active process of 'hypothesis testing'...

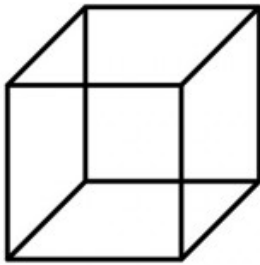
What we perceive is not invariably determined by what we see (i.e., by the image formed on the retina):

Ambiguous / bistable percepts;

Illusions of 3D depth;

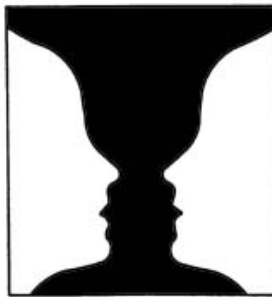
Prior assumptions about the scene

*



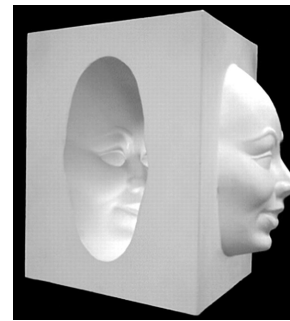
Necker Cube

*Swiss Crystallographer
Louis Necker (1832)*

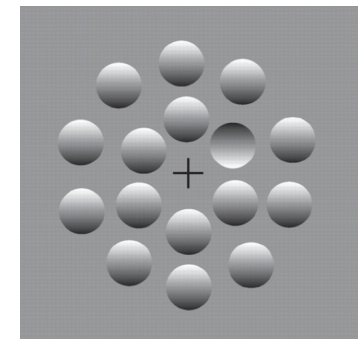


Rubin's Vase

*Danish psychologist
Edgar Rubin (1915)*

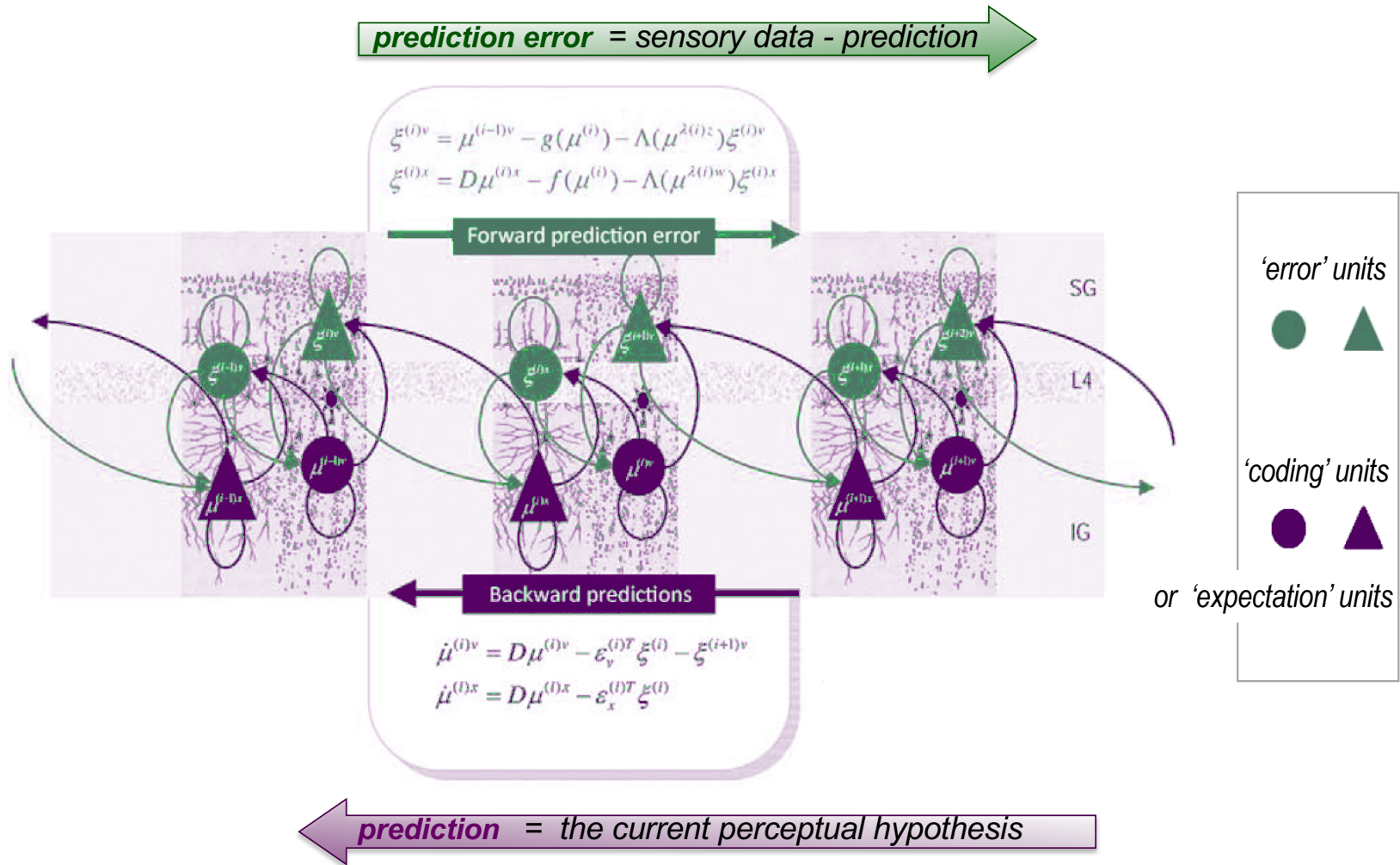


Face mask illusion



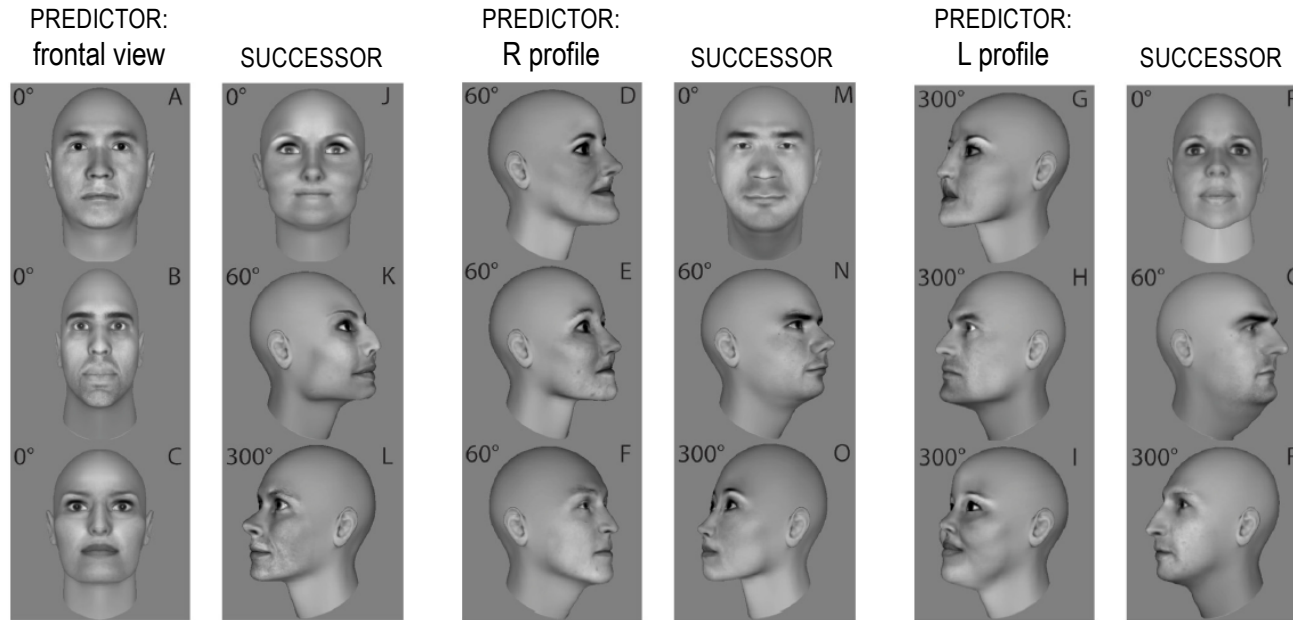
*'illumination from
above' prior*

Predictive Coding – an information processing theory requiring reciprocal exchange of forward & backward signals



Schwiedrzik & Freiwald (2017) [ref 16] *Neural signalling of prediction errors in face patch ML*

TRAINING



9 Training pairs
comprising face images of
3 different views (0° 60° 300°);
18 different identities (A-R).

30-day training period

TESTING

Predictor and successor stimuli were recombined in different pairings, creating violations of expected identity, expected view, or expected identity & view.

BUT – the authors classified these violations in terms of the predictor stimulus, as opposed to the successor stimulus; i.e. test stimuli were compiled such that the predictor “*differed from the successor’s original training partner in identity, view, or both*”. [- see examples on following slide].

Why is this wrong?

No violation of expectation occurs at the time of presentation of the predictor stimulus. Such violations only arise upon presentation of the successor stimulus. Predictive coding interprets the response of (some) cells to the successor stimulus as an ‘error’ signal, encoding its difference to the expected successor stimulus.

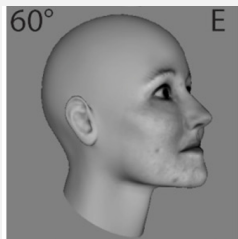
This is quite different to supposing that the response to the successor stimulus encodes a retrospective ‘error’ in the predictor stimulus, as required by the logic of the authors’ experimental design.

Authors' experimental logic

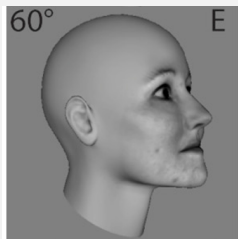
'expected' predictor
(given the tested successor)

trial type:

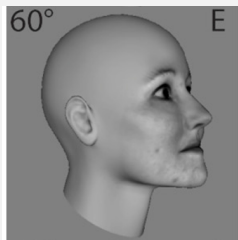
identity violation



view & identity violation



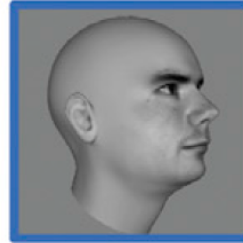
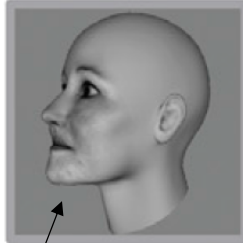
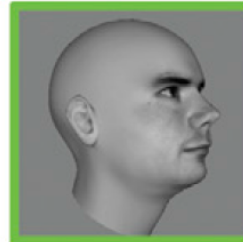
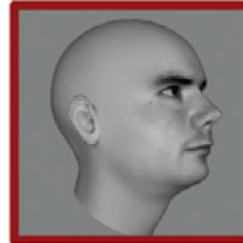
view violation



Example experimentally tested stimulus pairings

predictor

successor



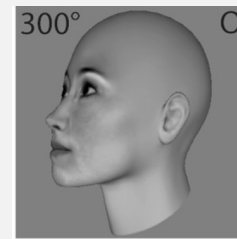
not a trained predictor, but its mirror-image...

Valid experimental logic !

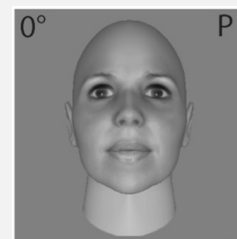
expected successor
(given the tested predictor)

trial type:

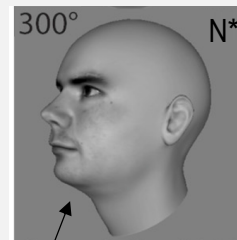
view & identity violation



view & identity violation



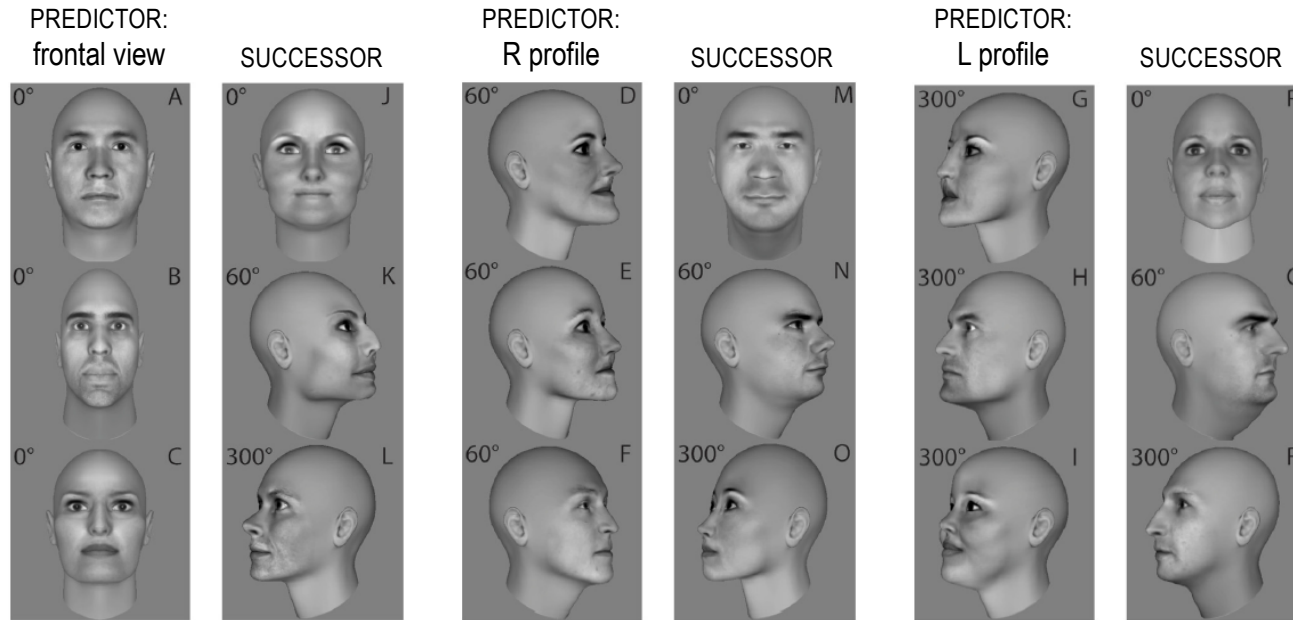
view violation ?



... so, possibly the monkey expects to see the mirror image of the expected identity ?

Schwiedrzik & Freiwald (2017) [ref 16] *Neural signalling of prediction errors in face patch ML*

TRAINING



9 Training pairs
comprising face images of
3 different views (0° 60° 300°);
18 different identities (A-R).

30-day training period

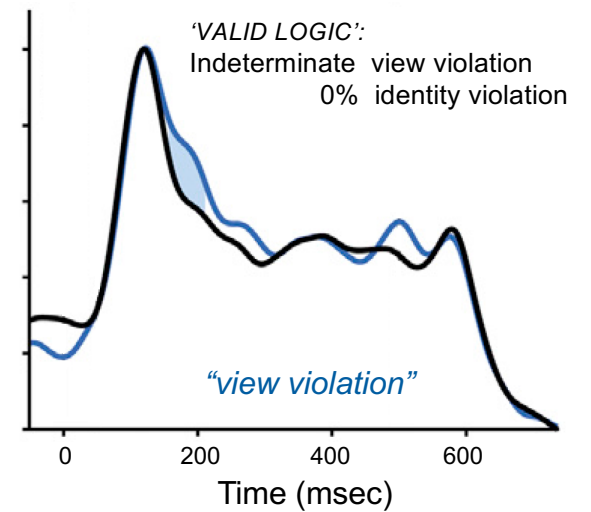
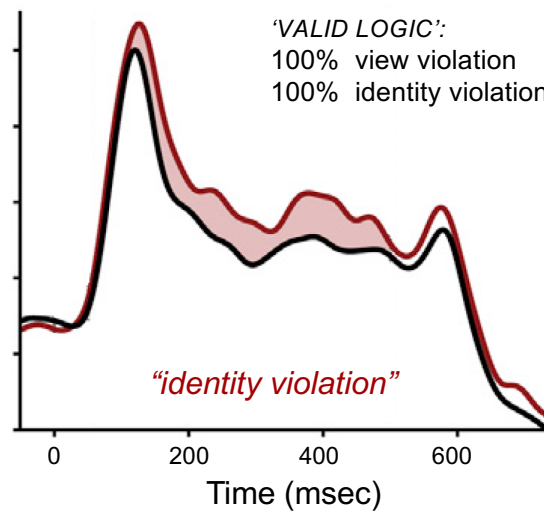
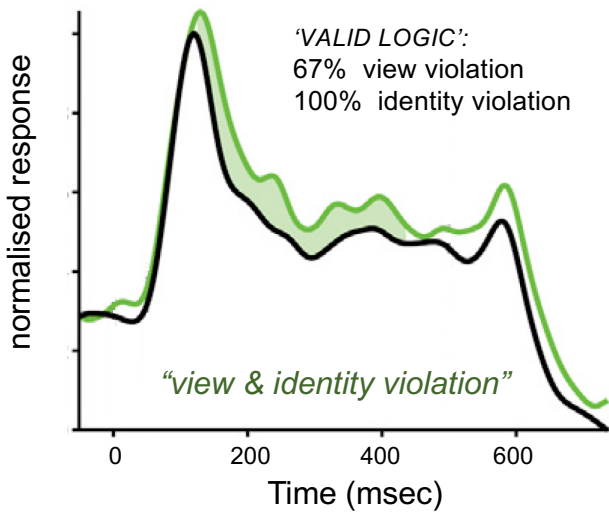
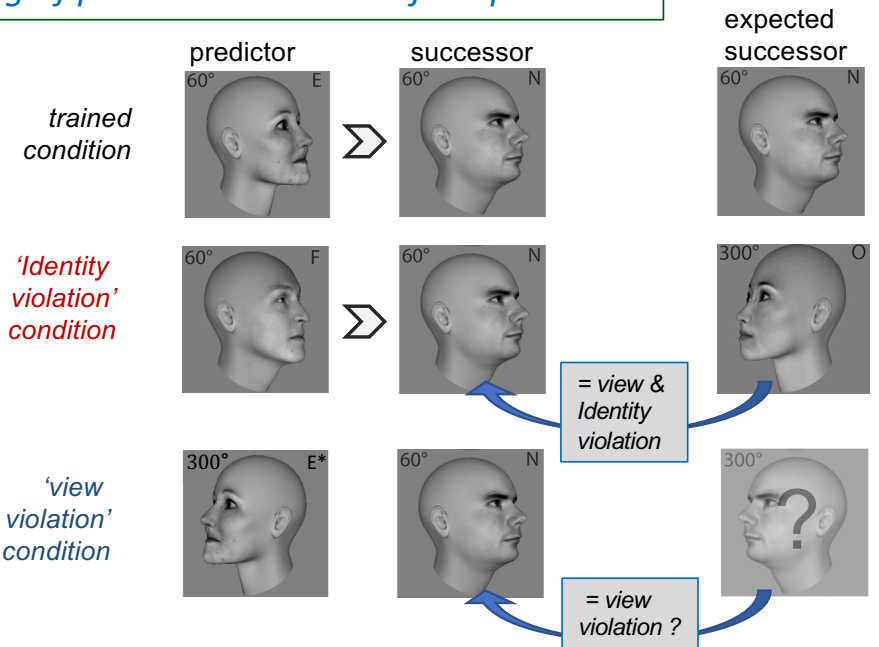
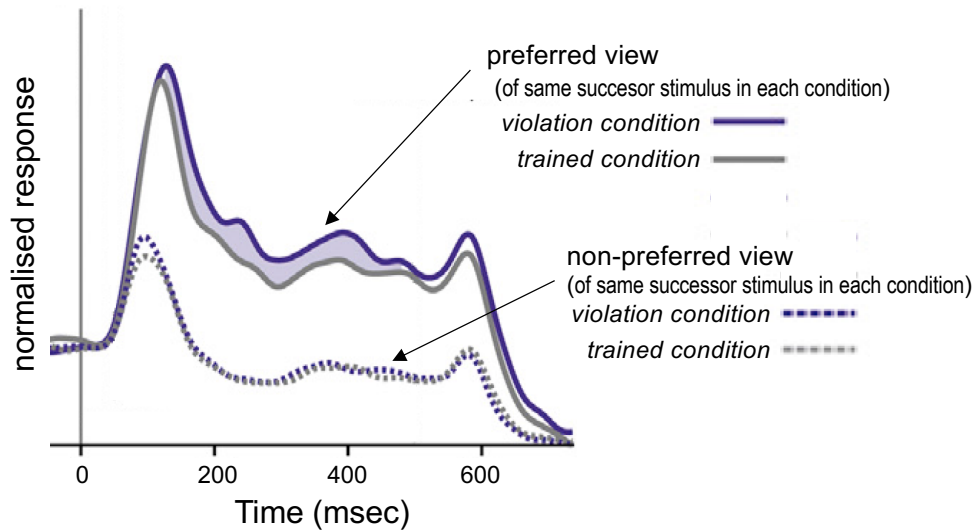
TESTING

EXPECTED PREDICTOR 'identity violation': e.g. authors used DN or FN in place of the trained pair EN;
- but D predicts M, and F predicts O, so these trials are actually 'identity & view violations', in terms of the EXPECTED SUCCESSOR;
- the same is found for all possible substitute predictors for all trained stimulus pairs;
- hence, all EXPECTED PREDICTOR 'identity violation' trials were 'view & identity violations', in terms of the EXPECTED SUCCESSOR.

EXPECTED PREDICTOR 'identity & view violation': e.g. authors used AN, BN, CN, GN, HN or IN in place of the trained pair EN;
- B and H predict the same 60° view as seen in N; but A, C, G and I predict a different view to N;
- the same 2:4 ratio of same : different is found for all possible substitute predictors for all trained stimulus pairs;
- hence, two-thirds of EXPECTED PREDICTOR 'view & identity violation' trials were equally 'view & identity violations', in terms of the EXPECTED SUCCESSOR, But one third of EXPECTED PREDICTOR 'view & identity violation' trials were 'identity violation' trials, in terms of the EXPECTED SUCCESSOR.

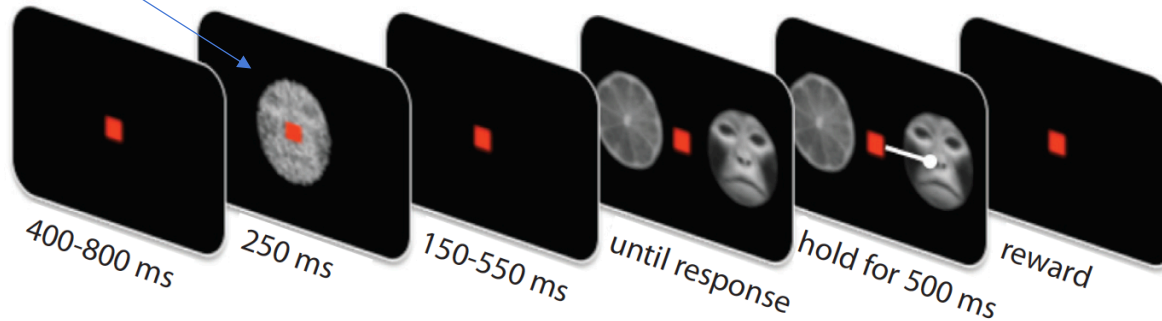
EXPECTED PREDICTOR 'view violation': e.g. authors used E*N (E* = mirror-image, or 300° version of E) in place of trained pair EN;
- similarly, D*M, F*O, G*P, H*G and I*R substitute a mirror-image view for the trained view;
- but A*J, B*K and C*L require substitution of a 60° or 300° profile in place of a 0° frontal view;
- none of A*, B*, C*, D*, E*, F*, G*, H* or I* are predictor face images used in training; the nature of the monkey's expectation is thus uncertain.
- hence, some of these trials might (or might not) act as view violation trials, in terms of the EXPECTED SUCCESSOR, but with weaker expectation at best.

Schwiedrzik & Freiwald (2017) [ref 16] Neural signalling of prediction errors in face patch ML

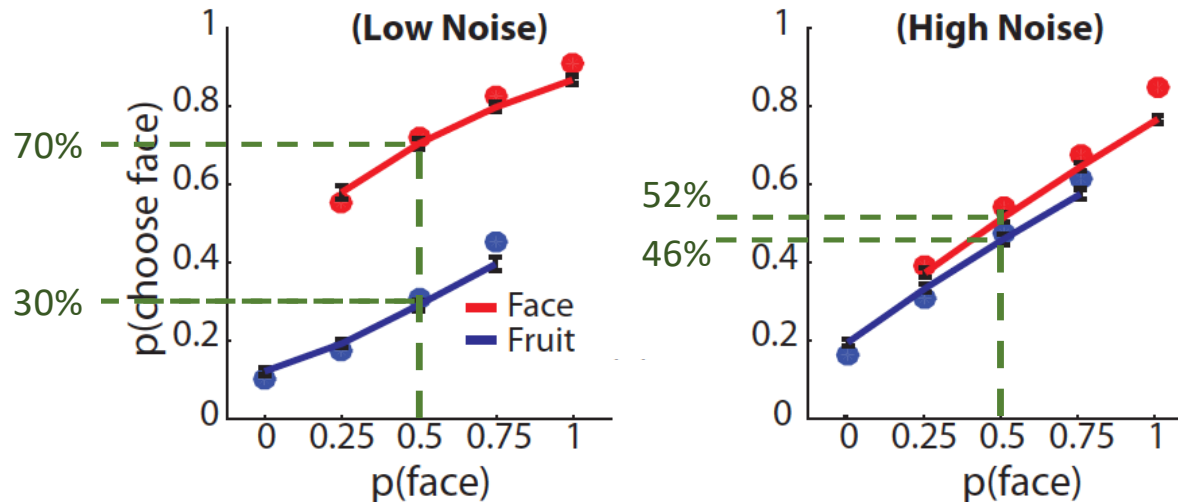


Bell et al. (2017) [ref 17] *Neural encoding of stimulus probability in inferior temporal cortex*

Low-noise
face stimulus



Task: monkey is shown an artificially degraded ('low-noise' or 'high-noise') image, of either a face or a fruit, and subsequently a choice display to indicate which it thinks it has seen. Correct responses are rewarded.



Plots of probability of selecting the 'face' option against probability that the cue stimulus was a face.

Behaviour

Trials were grouped in five blocks with varied probability of displaying the face stimulus: $p(\text{face}) = 0.0, 0.25, 0.5, 0.75$ or 1.0 .

The monkey 'learns' these probabilities, and adjusts its responses accordingly. E.g. in the high-noise condition it poorly discriminates face v fruit (52% correct selection of 'face' and 54% correct selection of 'fruit' at $p(\text{face}) = 0.5$) but the slope of the red and blue lines show that it does select the face more (or less) often in blocks with higher (or lower) $p(\text{face})$.

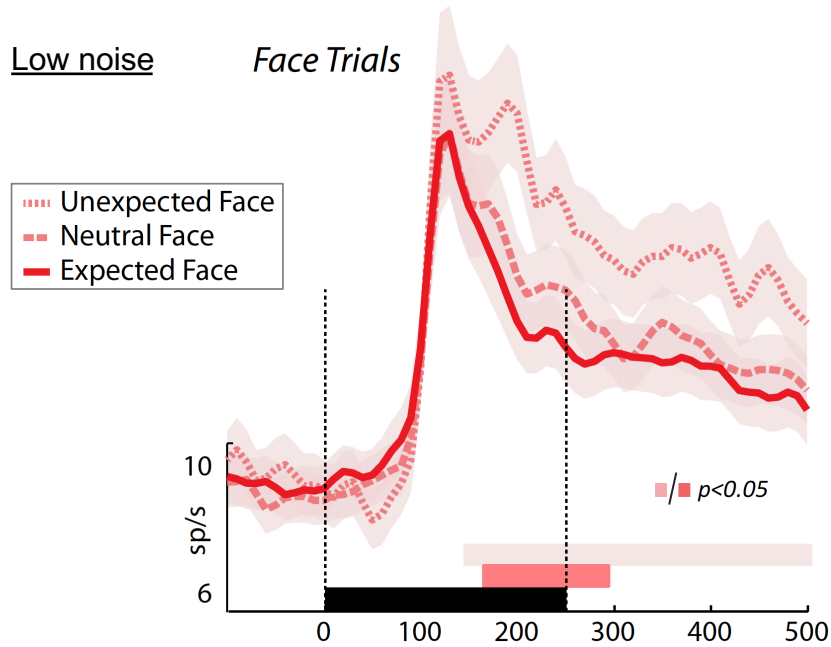
This demonstrates, behaviourally, that monkeys form an 'expectation' of seeing a face that adapts to the experimental regime.

Is it possible to find a neural encoding of this expectation ?

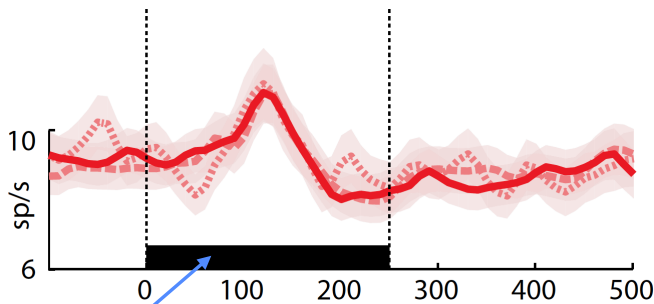
Bell et al. (2017) [ref 17] *Neural encoding of stimulus probability in inferior temporal cortex*

Low noise

Face Trials



High noise



Cue stimulus presentation period

Cell preferences in recorded population of IT cells :

61% face > fruit

1% fruit > face

38% no preference

However, the study does not identify the location of cells with respect to face patches ML, AL or AM. It presumably includes a mixture of cells inside and outside these patches.

Fluctuations in a monkey's behavioural expectation of seeing a face $p(\text{face})^*$ were modelled statistically from its face/fruit choices across trials.

Trials in which a face was presented are grouped into three classes:

Expected Face if $p(\text{face})^* > 0.66$

Neutral face if $0.66 > p(\text{face})^* > 0.33$

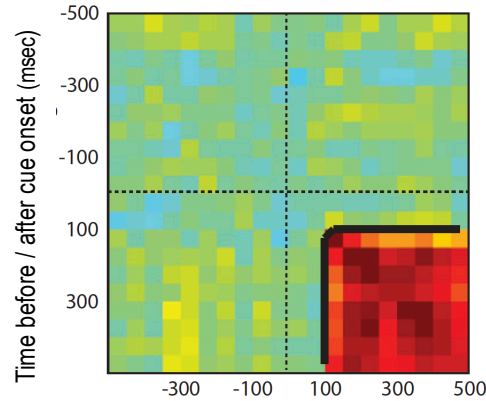
Unexpected Face if $p(\text{face})^* < 0.33$

Across the population, there was a greater response to unexpected faces than expected faces. This finding is consistent with the principle of predictive coding theory, that higher expectation of seeing a particular feature will act to reduce the response of ERR units reporting that feature to higher areas. Note that this was only observed for low noise stimuli, not high noise stimuli.

But, not all cells should be ERR units: predictive coding theory envisages that some cells explicitly encode expectations (EXP units). Is it possible to discriminate EXP and ERR units..?

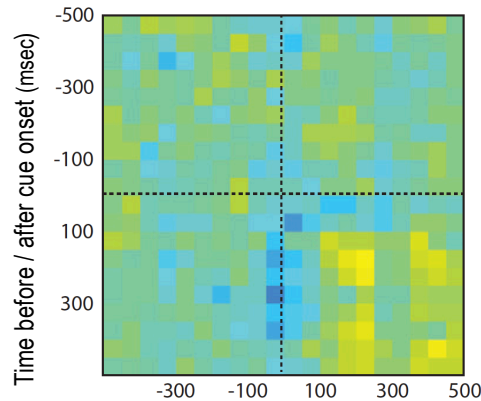
Bell et al. (2017) [ref 17] *Neural encoding of stimulus probability in inferior temporal cortex*

face v fruit preference



Prediction error

p(face)*



Prediction error

Time before / after cue onset (msec)

Regression analysis was used to model, for each cell, the contribution of three factors to variation in the cell's response across all trials:

- Stimulus preference for face v fruit;
- Prediction error, the discrepancy between expectation and the actual stimulus presented;
- The level of expectation of seeing a face, $p(\text{face})^*$

$$\text{spike rate} = \beta_0 + \beta_1 \cdot \text{stimulus} + \beta_2 \cdot \text{error} + \beta_3 \cdot \text{expectation}$$

The relative values of the β_1 , β_2 and β_3 coefficients of these three factors vary with changes in a cell's spike rate before and after cue presentation.

The charts at left show correlations between these coefficients across the population of recorded cells; the correlation was computed for all possible pairs of time points between -500 and +500 msec from stimulus onset.

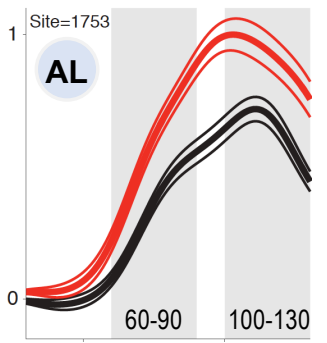
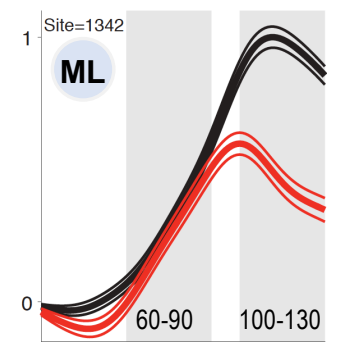
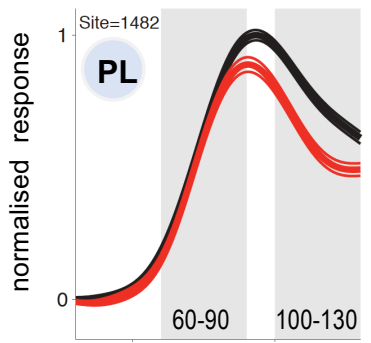
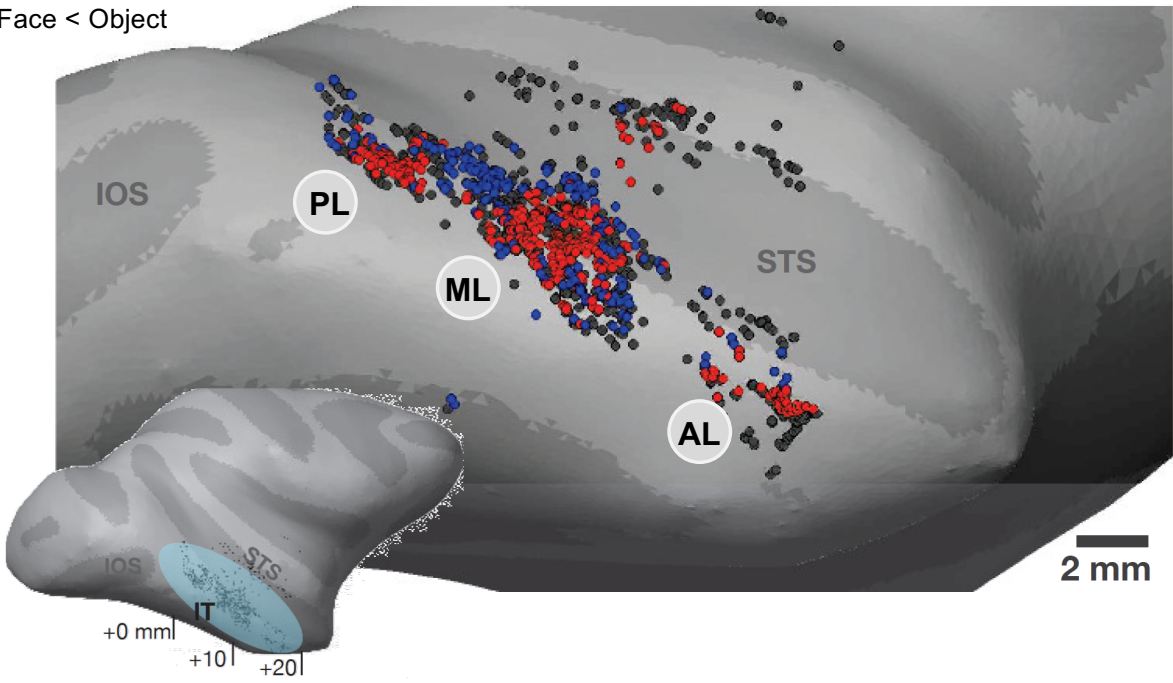
Upper chart: Encoding of face prediction error and stimulus identity were highly correlated from 100 msec onward in the post-stimulus period; or, in other words, "neurons that showed the strongest face responses also showed the greatest difference in response magnitude between expected and unexpected face trials".

Lower chart: Conversely, over the same time period, there is no significant correlation between the extent to which neurons encode face prediction error and face expectation.

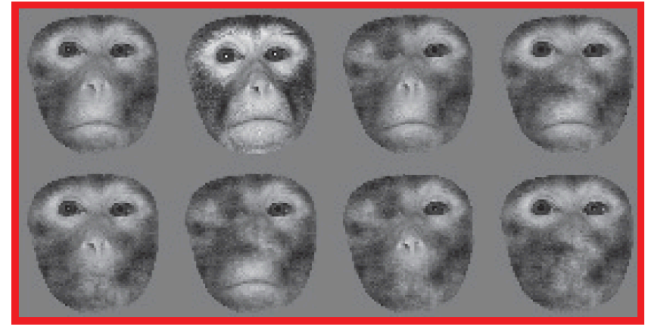
The second finding is consistent with the predictive coding principle that distinct populations of neurons encode predictions and prediction-errors (i.e. EXP v ERR units). However, this is an indirect indication derived from population statistics; the study did not succeed in explicitly identifying individual neurons as EXP or ERR units.

Issa *et al.* (2018) [ref 15] *Error responses to 'scrambled' face stimuli*

- Face > Object
- Face < Object

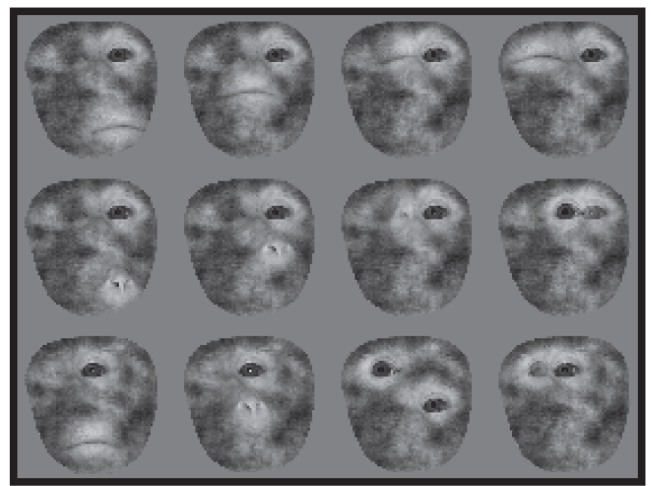


TYPICAL



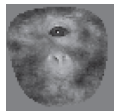
Typical arrangement of facial features

ATYPICAL

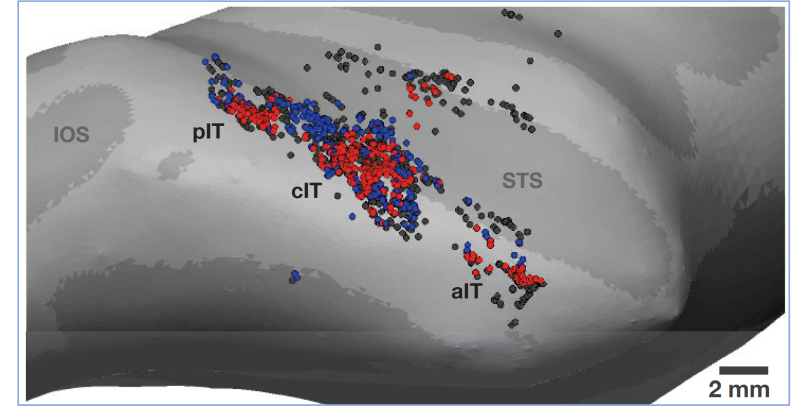
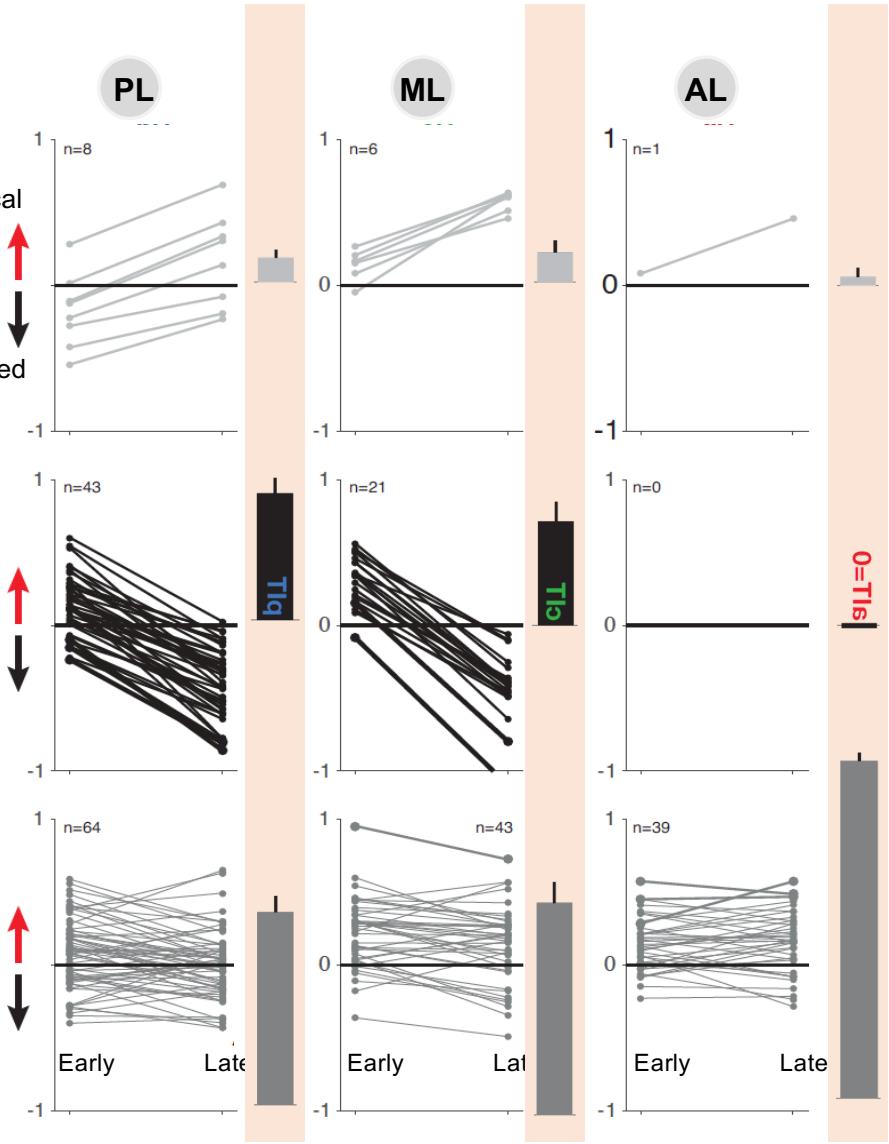


Scrambled facial features

Issa *et al.* (2018) [ref 15] Error responses to 'scrambled' face stimuli



prefer typical
↑
↓
prefer scrambled



= error coding, 'ERR' units

= prediction or expectation coding, 'EXP' units ?

Summary of these three face-processing studies formulating their findings in terms of predictive coding theory

Schwiedrzik & Freiwald (2017) Manipulate the animal's state of expectation by training it to recognise sequentially presented pairs of face stimuli varying in view and identity. They find that expected stimuli can elicit smaller responses than unexpected stimuli, as anticipated for cells signalling prediction errors (ERR units). However:

1. Unaccountably, they mis-classify the types of violation of expectation present in their test stimuli. This requires some guesswork to re-classify violations, but it is then possible to re-interpret their findings as showing that (some) ML cells respond as if signalling error with respect to expected view, but irrespective of expected identity.
2. Not all cells should be ERR units, but there is no systematic documentation of individual cell response properties (that might enable non-ERR units to be distinguished);
3. The authors' account of predictive coding theory (possibly influenced by their procedural error) largely neglects theoretical sources, and is highly misleading !

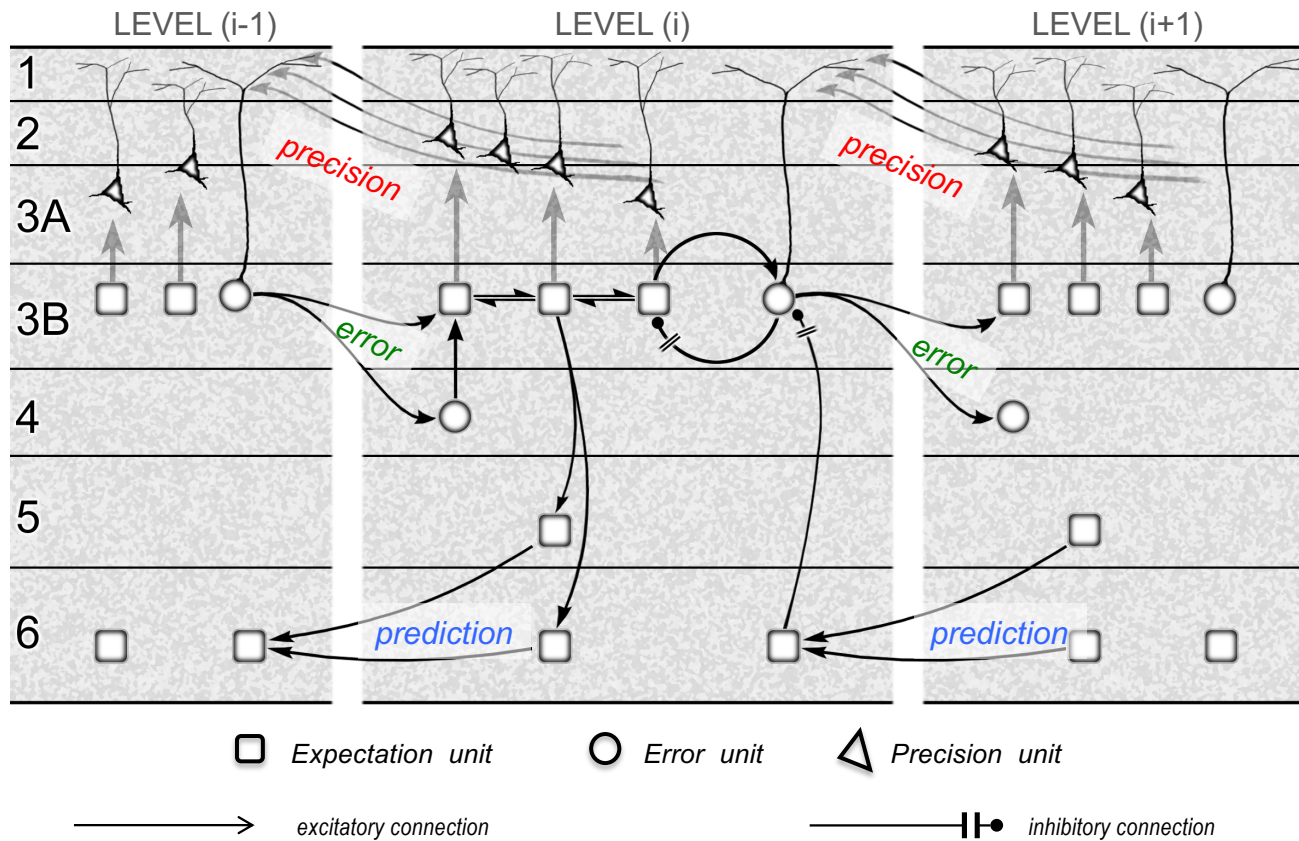
Bell et al. (2017) Manipulate the animal's state of expectation by presenting stimuli in blocks that vary in their relative frequency of showing a face (or a fruit). They also demonstrate that unexpected face stimuli produce larger responses, on average, across the population of recorded cells – again, as anticipated for cells signalling prediction errors. These authors, however, are aware that predictive coding theory does not propose that all cells should signal prediction error. Some should encode expectation (EXP units).

1. They use a sophisticated regression model to assess cells' encoding of stimulus identity, the animal's pre-stimulus state of expectation, and post-stimulus error.
2. This demonstrates that, across the population of recorded cells, there is little or no correlation between encoding of error and expectation; but no individual cells were identified explicitly as ERR or EXP units.

Issa et al. (2018) This study is the only one of the three to record from several identified levels in the face hierarchy. It did not manipulate the animal's state of expectation *per se*. It attempted to measure the influence of 'prediction' in the sense of the current description of a visual stimulus provided by backward connections from higher areas to lower areas. This represents a more naturalistic way of testing predictive coding theory.

1. It finds that a more 'surprising' (scrambled) face stimulus elicits less activity than a normal face in the highest face area, but can elicit more activity than a normal face in some cells in two hierarchically lower face areas.
2. This finding is, once again, consistent with the predictive coding principle that backward-going signals should suppress activity in ERR units in a lower area. These signals, in theory, are provided by EXP units in the highest area.
3. The greater activity in these (putative) ERR units can be rationalised as signalling how the scrambled face stimulus deviates from the prediction (or 'description') of a normal face communicated by the highest area.
4. This error-signal, when present, was strongest at 100-130 msec post-stimulus onset; Cells that failed to show this signal but which, conversely, showed a growing preference for the normal face stimulus over the scrambled face stimulus, at 100-130 msec, can be regarded as putative EXP units.

Schematic model of intrinsic & extrinsic wiring subserving predictive coding:
 reciprocal exchange of **prediction** & **precision** (backward) & **error** (forward)
 - e.g. as modelled by serial hierarchical connections between sensory cortical areas



Note on neural implementation of predictive coding (previous slide)

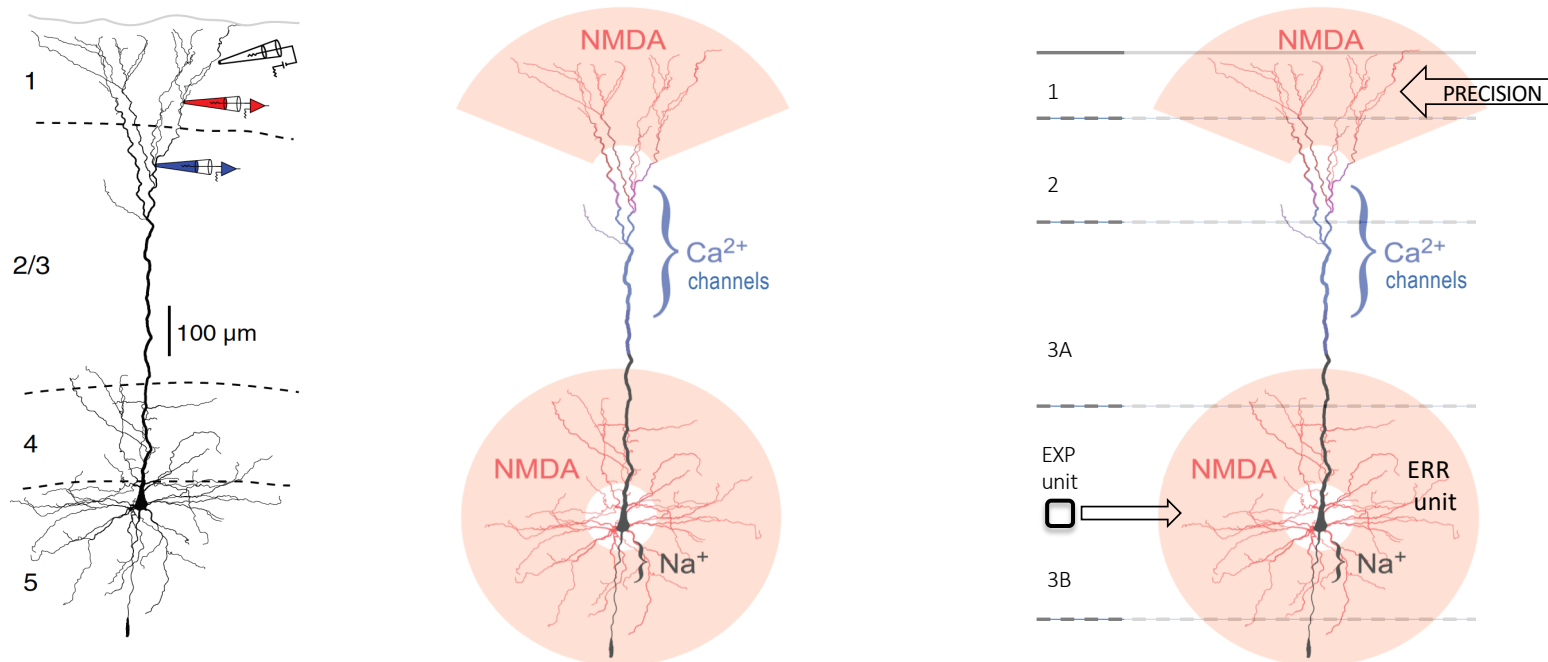
1. This is all rather conjectural, an exercise in fitting the theoretical computational procedures of predictive coding to the known patterns of intrinsic and extrinsic connectivity of the cortex.
2. The fundamental idea underlying predictive coding is that all perception is a guess (or hypothesis) – it has to be, because the retinal image never provides information adequate to specify exactly what is present, where, in the visual field.
3. This ‘guessing’ is formalised as *Bayesian inference*: that what we perceive is ultimately a combination of sensory evidence and prior knowledge, statistically optimised to trade off the the reliability of the sensory evidence against the weight of the expectation based on prior experience.
4. The basic computational mechanism is that backward connections convey predictions (blue), and forward connections convey prediction error (green); a second class of backward connection conveys ‘precision’ (red).
5. Correspondingly, there should be three discernible classes of pyramidal neurons: *expectation* (EXP) and *precision* units that are the source of back projections, and *error* (ERR) units that are the source of forward projections.
6. The signals carried by the backward projections of EXP units can be regarded as predictions of the activity of EXP units at the level below.
7. The ERR units within a level compute the difference between the EXP units in the same level, and the prediction arriving from the level above. The ERR signal is conveyed to the level above, where it modifies the activity of the EXP units at that level.
8. A simpler way of thinking about this is that the ERR units compute the difference between the sensory data reaching an area and the prediction of that data provided by higher areas. Note that the difference is computed as a simple subtraction (data – prediction), so the prediction should reach the ERR units via an inhibitory intrinsic relay.
9. The combined activity of EXP units across areas determines our percept of the image on the retina; the activity of ERR units has the effect of modifying that percept.
10. *Precision* is a term used to describe the gain of the ERR signal (i.e. the ERR signal is boosted by high precision, and attenuated by low precision). Precision therefore regulates the balance between expectation and sensory evidence (data) in determining what we see.
11. The various examples given of a prior hypothesis governing what we see, to resolve ambiguity or even to produce an illusion (e.g. that light comes from above, that staircases do not have gaps, and that vertebrate heads are convex, not concave structures) would be rationalised as circumstances where the prior hypothesis is very strong, and the precision applied to the ERR signal is not strong enough to allow contrary sensory evidence to modify the representation of the hypothesis by EXP units in high level visual areas.

Glossary

Intrinsic connections are those within an area, extrinsic connections are those between areas

Pyramidal neurons are excitatory (i.e. use an excitatory neurotransmitter) as opposed to inhibitory interneurons

Larkum et al (2009) Control of pyramidal neuron excitability by backward terminations upon apical dendrite [ref 18]



1. Multiple, in vitro, intracellular recordings from pyramidal neurons with cell bodies in layer 5;
2. Spiking activity in the cell is initially activated by forward input to basal dendrites;
3. Spikes (action potentials) also 'back-propagate' into the apical dendritic tree (causing depolarisation);
4. NMDA glutamate receptors in the apical dendritic arborisation require some initial depolarisation in order to become sensitive to backward inputs;
5. The combined effect of backward input and back-propagation can 'ignite' Ca channels situated in the base of the apical tuft;
6. The Ca channels can drive further cell spiking, and render the cell much more sensitive to continued forward input.
7. Larkum describes this as a 'coincidence-detection' mechanism for the simultaneous arrival of forward and backward input;
8. In terms of predictive coding theory, it allows backward signals to regulate the amplification, or 'gain' of forward signals, as envisaged for precision. This is termed 'apical amplification'.

Interpretation of the Larkum mechanism in the context of the neural implementation of predictive coding theory: Layer 3 pyramids postulated to be similar to layer 5 pyramids; putative ERR units in layer 3 receive signals from EXP units in their basal dendrites, and descending precision signals in their apical dendrites