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# Of Primates, Faces, and Intelligence

## Winrich Freiwald, PhD



SCIENCE FOR THE BENEFIT OF HUMANITY

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# Octopus

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copyright restrictions. Please see lecture  
video.

# **Octopus**

Photos of the life cycle of an octopus  
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Please see lecture video.

# Wildebeest

Photo of wildebeest migration removed due  
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video.

# Primates

## The Social Intelligence Hypothesis

*Marais, Chance, Jolly ...*

*Nick Humphrey (1976)*

*"The social function of intellect"*

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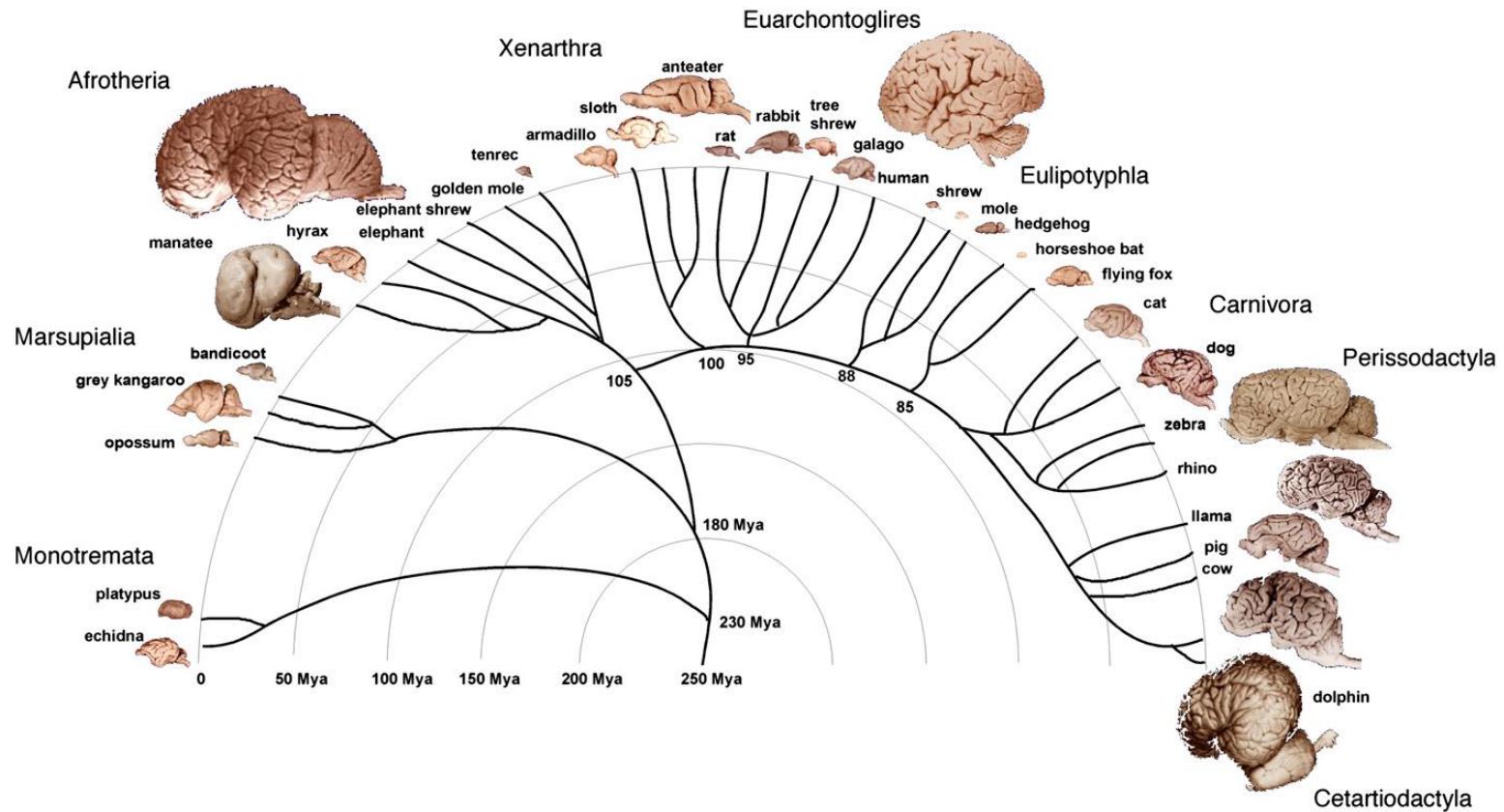
# The Primates

- Monophyletic mammalian order, 400 plus species
- Highly diverse (30g to 200kg)
- ~65-85 mya
- All species social
- Slow development, long lifespan
- Visual (binocular) rather than olfactory
- Larger brains relative to other mammals

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Please see lecture video or the phylogenetic tree of mammals on page 87 of Allman, John Morgan. Evolving brains. New York: Scientific American Library, 2000.

# Mammalian Brains



Courtesy of National Academy of Sciences, U.S.A. Used with permission.  
 Source: Herculano-Houzel, Suzana. "The remarkable, yet not extraordinary, human brain as a scaled-up primate brain and its associated cost." *Proceedings of the National Academy of Sciences* 109, no. Supplement 1 (2012): 10661–10668.

# Vertebrate, Mammalian, and Primate Brains

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Please see lecture video or the graph of vertebrate brain to body weight on page 19 of Allman, John Morgan. *Evolving brains*. New York: Scientific American Library, 2000.

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Please see lecture video or the graph of mammalian brain to body weight on page 161 of Allman, John Morgan. *Evolving brains*. New York: Scientific American Library, 2000.

# Primate & Mammalian Brains

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from Herculano-Houzel, Suzana.

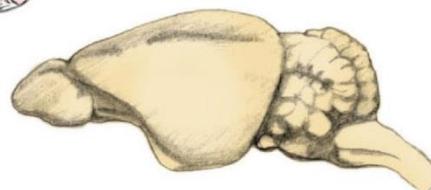
"Brains matter, bodies maybe not: the  
case for examining neuron numbers  
irrespective of body size." Annals of  
the New York Academy of Sciences  
1225, no. 1 (2011): 191-199..

# Primate & Mammalian Brains

## Rodents

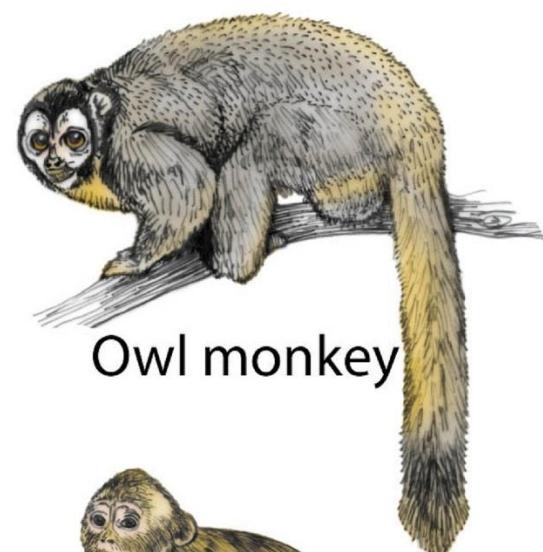


Agouti



18 g    857 M  
neurons

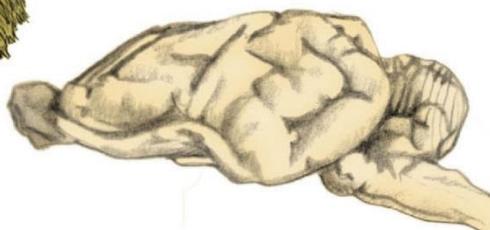
## Primates



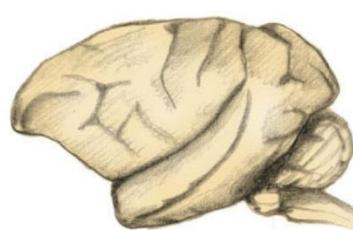
Owl monkey



Capybara



76 g    1600 M  
neurons



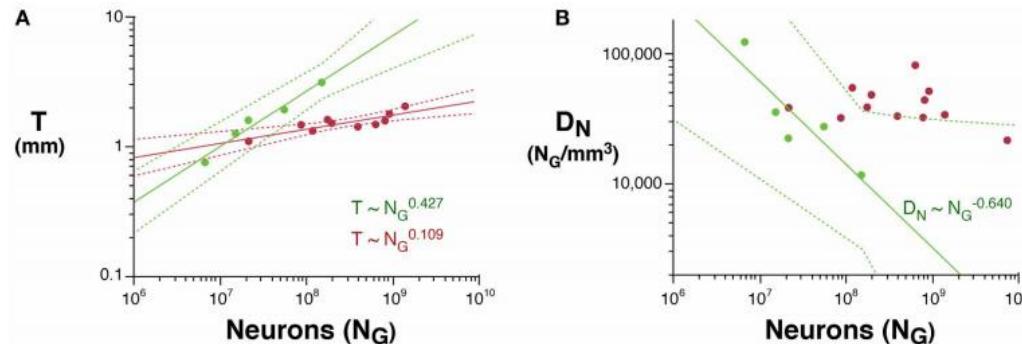
52 g    3690 M  
neurons



Capuchin monkey

Courtesy of Suzana Herculano-Houzel, license CC BY.  
Source: "The human brain in numbers: A linearly scaled-up  
primate brain. "Frontiers in human neuroscience 3 (2009): 31.

# Primate & Mammalian Brains



**FIGURE 2 |** Scaling of average cortical thickness (A) and of average neuronal density (B) as a function of numbers of cortical neurons in rodents (green) and primates (red). Power functions, where the exponents

are significant at the level of  $p < 0.05$ , are plotted for each mammalian order with the respective 95% confidence intervals (dotted lines). Exponents are indicated.

Courtesy of the authors, license CC BY.  
 Source: Ventura-Antunes, Lissa, Bruno Mota, and Suzana Herculano-Houzel. "Different scaling of white matter volume, cortical connectivity, and gyration across rodent and primate brains." *Frontiers in neuroanatomy* 7 (2013): 3.

- Cortical thickness scales up with neural number faster in rodents than in primates
- **Neuron size is increasing with brain size in rodents, not much in primates**
- Neural density higher in primates than in rodents
- Per cortical neuron #, primates need less white matter volume than rodents
- **White matter fiber caliber increases with brain size in rodents, hardly in primates**
- Relatively larger cortex/cerebellum fraction in primates than in rodents
- **Primate brains fold faster with increasing size than rodent neurons**

# The Primates: Anatomy

- Forward facing eyes, binocular vision, color vision
- Skull with large cranium
- Opposable thumbs
- Highly mobile shoulder (dorsal positioning of scapula)
- “Trend” towards reduced snout

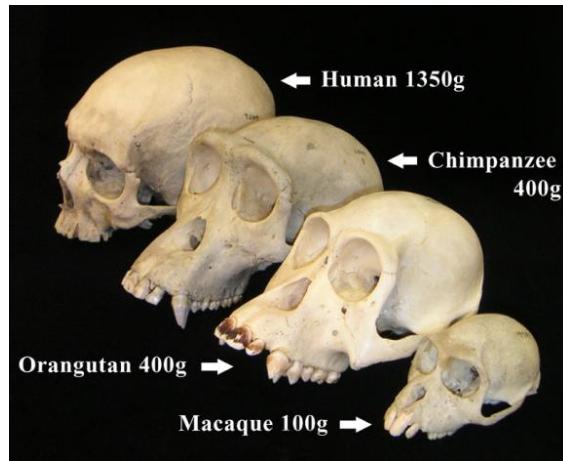


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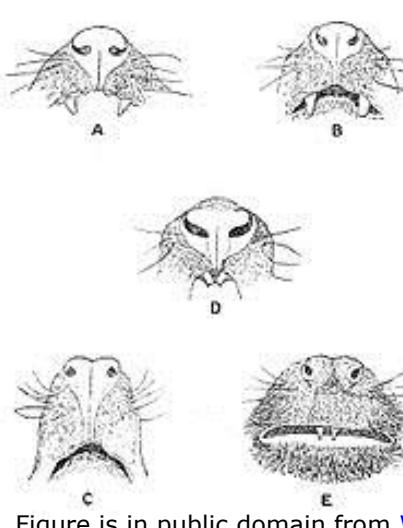
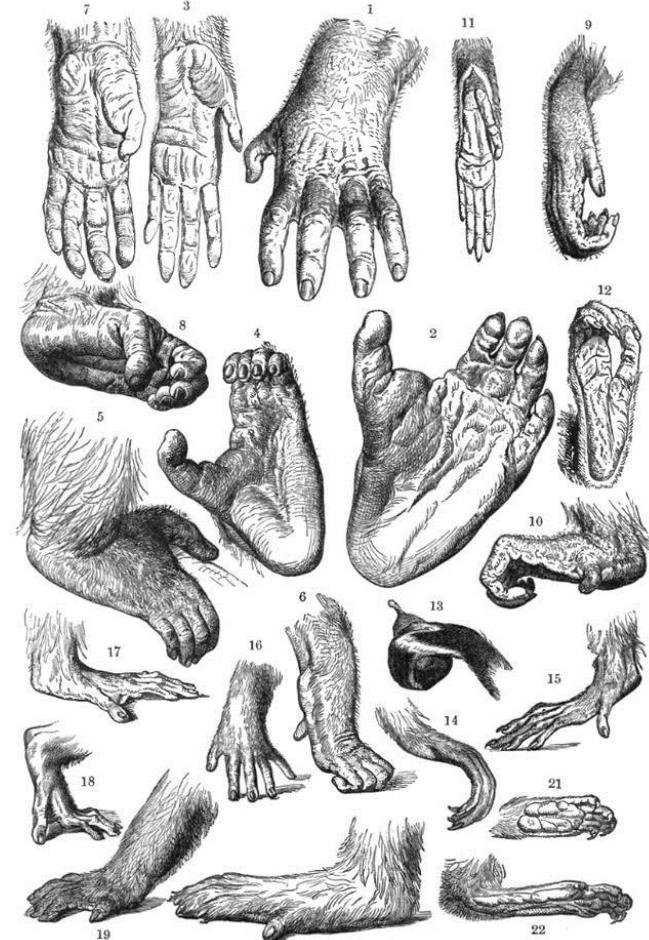


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HANDS AND FEET OF APES AND MONKEYS.  
1, 2, Gorilla ; 3-8, Chimpanzee ; 9, 10, Orang ; 11, 13, Gibbon ; 14, 15, Guereza ; 16-18, Macaque ;  
19, 20, Baboon ; 21, 22, Marmoset.

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# The Primates: Sociality

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Four main organizations of social life

- Female transfer system (spider monkeys)
- **Male transfer system:** polygonous & multi-male (capuchin, old-world monkeys: macaques, baboons)
- Monogamous (gibbons)
- Solitary (male defending territory, slow loris, orangutan)

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Social behavior of **cooperation** (grooming, defense, hunting) & **competition** (food, mates, dominance hierarchies)

# Primate Social Life

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Please see lecture video or Cheney, Dorothy  
L., and Robert M. Seyfarth. *Baboon  
metaphysics: the evolution of a social mind.*  
University of Chicago Press, 2008.

# The Social Intelligence Hypothesis

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Please see lecture video or Cheney, Dorothy  
L., and Robert M. Seyfarth. *Baboon  
metaphysics: the evolution of a social mind.*  
University of Chicago Press, 2008.

# The Social Intelligence Hypothesis

- We do not know whether social intelligence is primate-specific.
  - social complexity could be high in other species that live in complex societies comprised of multiple families and stable dominance hierarchies like dolphins (*Tursiops truncates*), elephants (*Loxodonta africana*), spotted hyenas (*Crocuta crocuta*). Maybe these individuals, too, recognize and monitor other individuals' social relationships?
- Are primate societies more complex than those of other taxa?
- Within the primate order, social learning, innovation, and tool use are strongly correlated with brain size, not group size (Reader 2003):
  - Chimpanzees, orangutans, and capuchin monkeys have larger brains than other primates and use and manufacture tools more routinely than monkeys, but live in relatively small groups. Indeed, orangutans are frequently solitary.
  - Thus tool use and behavioral flexibility, not the complexity of social groups might have driven brain evolution in primates.



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# **Primates are social – and invent cool tools**

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“L’Univers social des macaques.” Filmed  
January 1990. Video, 00:26.

[http://www.canal-  
u.tv/video/cerimes/l\\_univers\\_social\\_des\\_macaques.9257](http://www.canal-u.tv/video/cerimes/l_univers_social_des_macaques.9257).

# The Social Intelligence Hypothesis

- We do not know whether social intelligence is primate-specific.
- Are primate societies more complex than those of other taxa?
- Within the primate order, social learning, innovation, and tool use are strongly correlated with brain size, not with group size (Reader 2003)
- Are primates' abilities in social knowledge really intelligent or just idiot savant-like abilities?

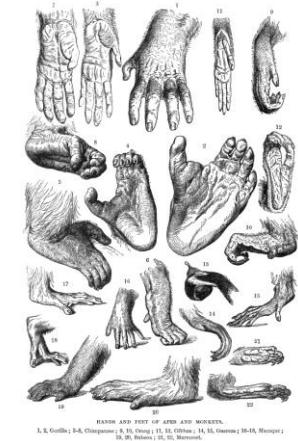


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# Social Knowledge in Baboons

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## Is it knowledge or just extensive associations?

- 80 individuals: 3,160 dyads & 82,160 triads
- Relationships can change fast
- no single behavioral metric is necessary or sufficient to recognize associations like matrilineal kin (human observer using counts of aggressive or grooming behavior cannot infer relationships)
- Social relationships like friendship are intransitive, others like family-relationships are non-associative
- Simultaneous membership in multiple classes possible

# The story of Ahla (*Papio ursinus ruacana*)

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# The story of Ahla (*Papio ursinus ruacana*)

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Hoesch, W. “Uber Ziegen hiitende Barenpaviane  
(*Papio ursinus ruacana* Shortridge).” (1961).

# Structure of Primate Social Knowledge

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# from Neurons to Minds

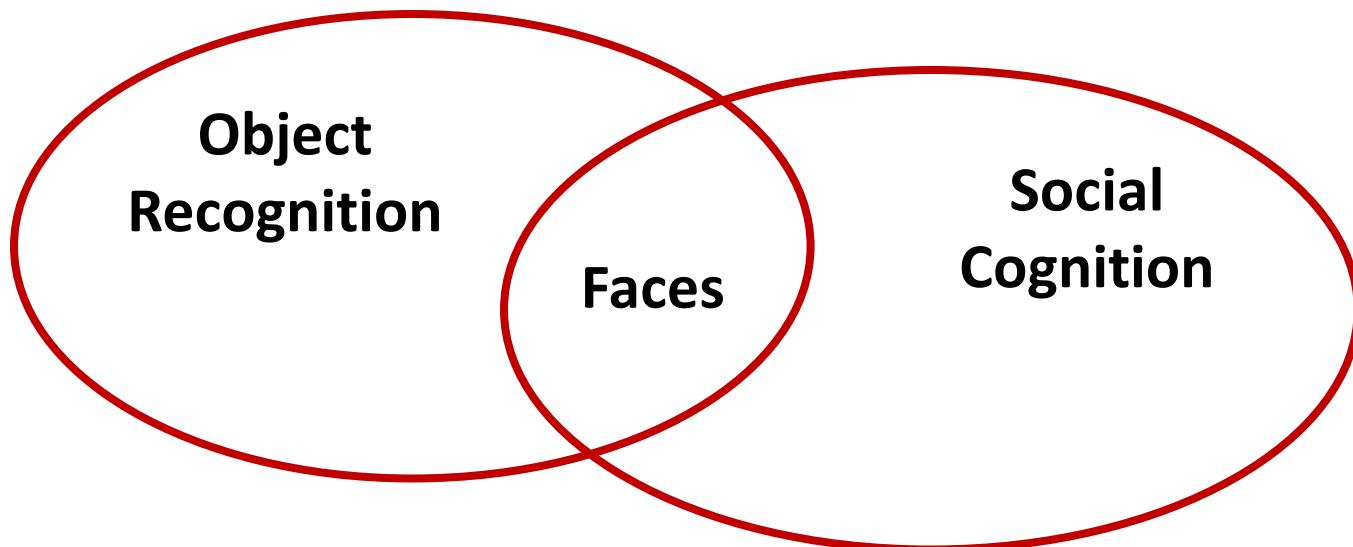


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Daniel J., and David C. Van Essen. "Distributed  
hierarchical processing in the primate cerebral  
cortex." *Cerebral cortex* 1, no. 1 (1991): 1-47.

# Gestalt Rules of Perception

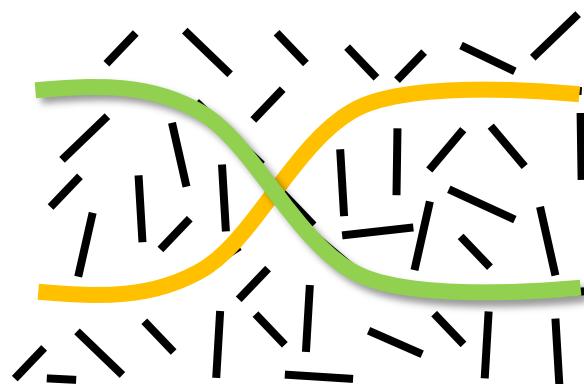
Proximity



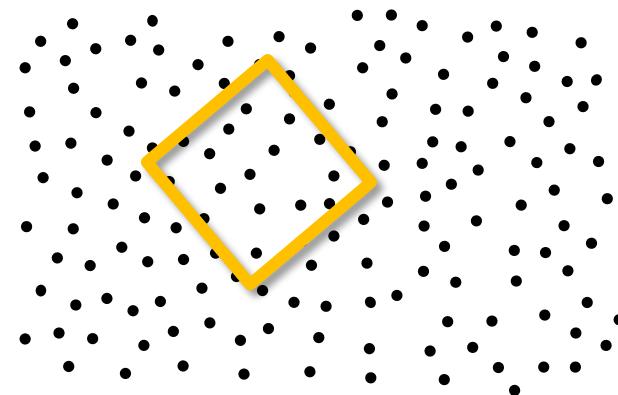
Similarity



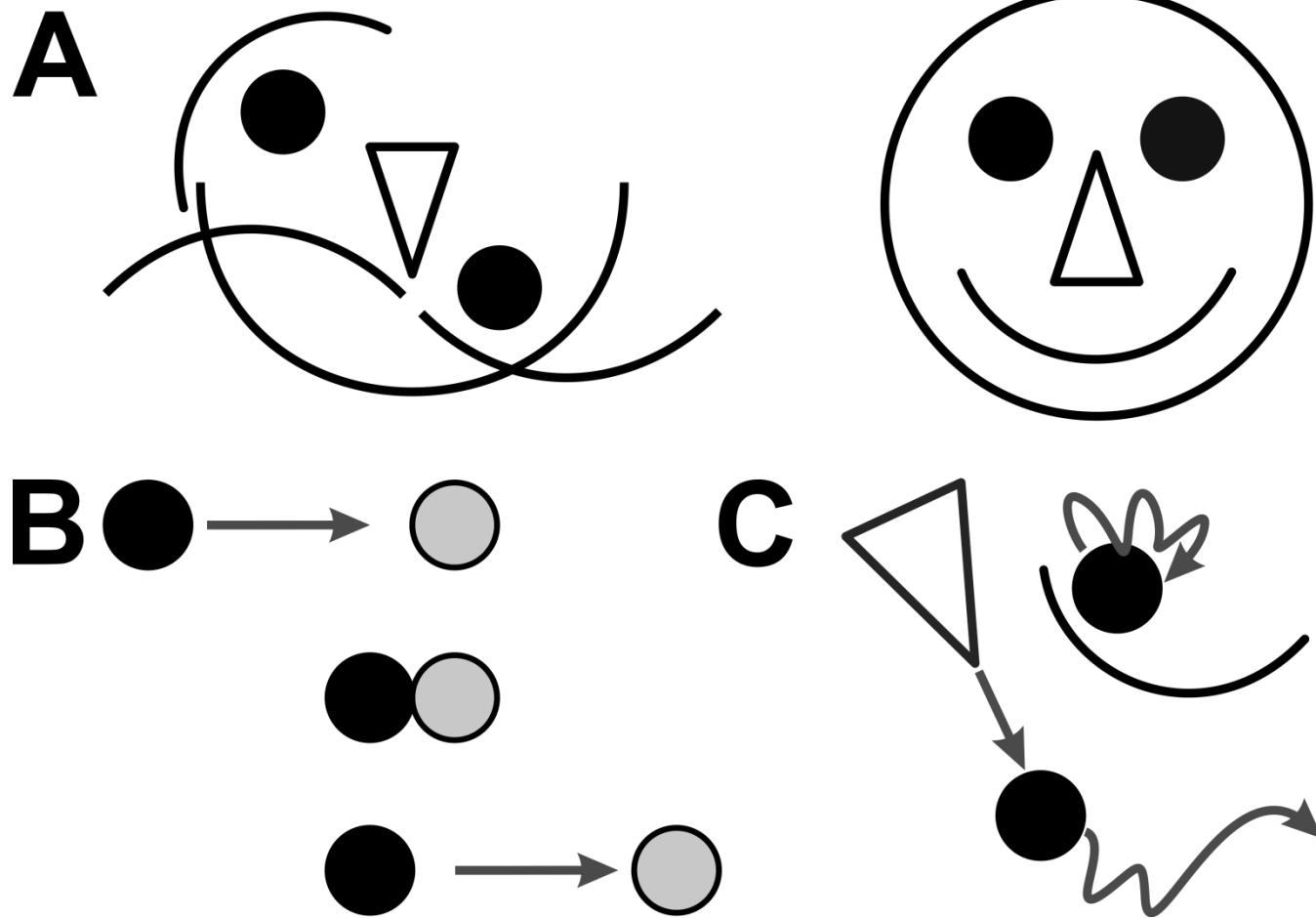
Good Continuation



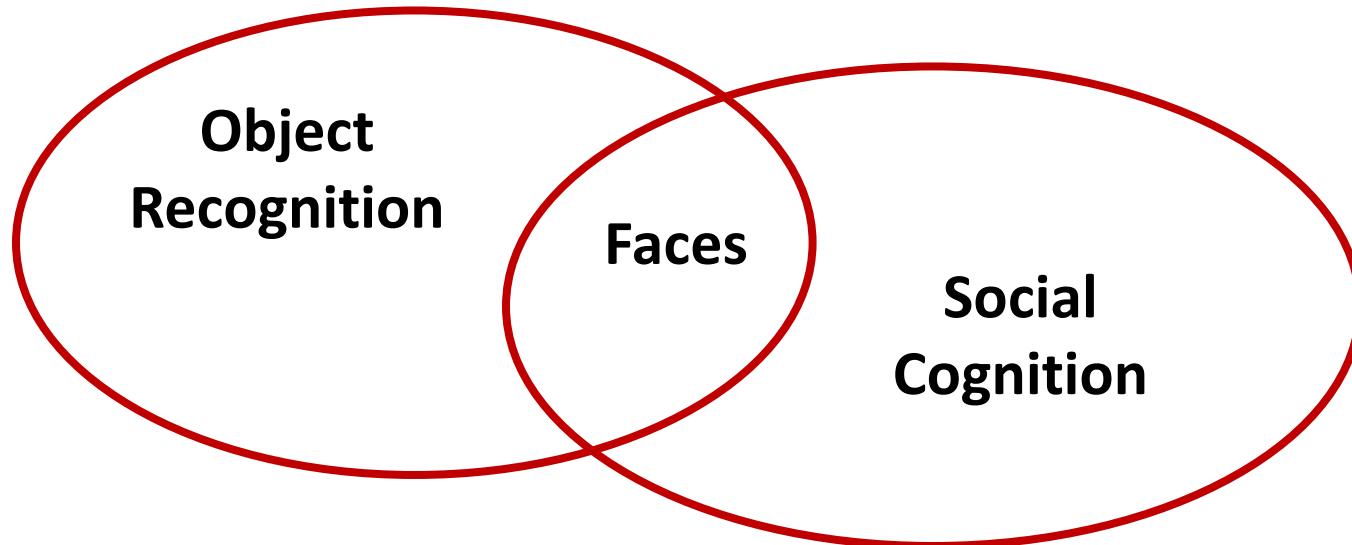
Common Fate



# Internal Models of Perception



# from Neurons to Minds



- Constructive process
- Not just collection of features: unit of cognition
- Basis of Symbolic Representations
- Creates Meaning
- Makes information actionable

# **Primates are social**

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“L’Univers social des macaques.” Filmed  
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# The Expression of the Emotions in Man and Animals

## Charles Darwin, 1872



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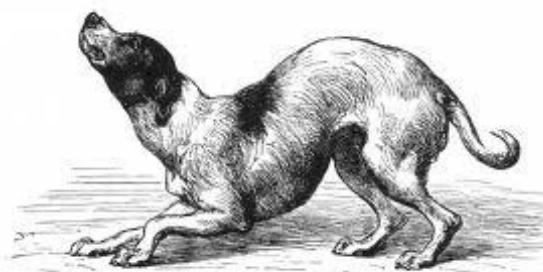


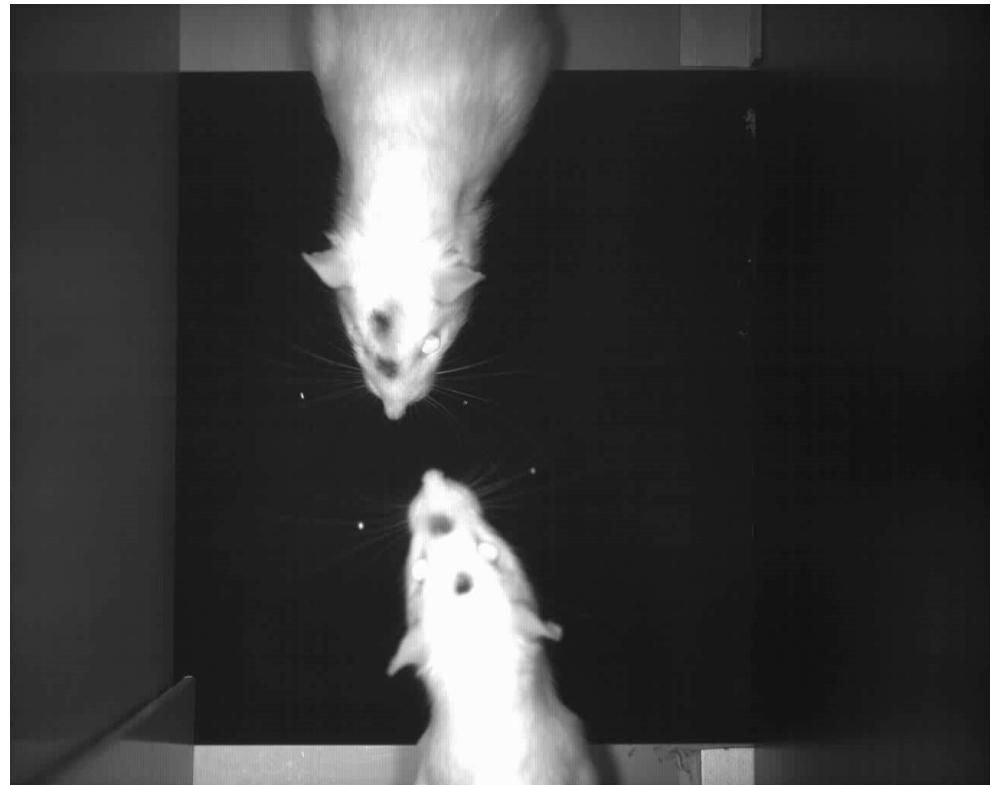
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# Facial Communication (and lack thereof)

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Photo of a frog sitting on a bench removed due to copyright restrictions. Please see lecture video.



## Facial interactions in rats - from Bobrov & Brecht

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Source: Bobrov, Evgeny, Jason Wolfe, Rajnish P. Rao, and Michael Brecht. "The representation of social facial touch in rat barrel cortex." *Current Biology* 24, no. 1 (2014): 109-115.

# Facial Communication in Primates

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Lisa A., Bridget M. Waller, Anne M. Burrows,  
Katalin M. Gothard, and Sarah-Jane Vick. "Brief  
communication: MaqFACS: A muscle-based  
facial movement coding system for the rhesus  
macaque." American journal of physical  
anthropology 143, no. 4 (2010): 625-630..

# Facial Communication in Primates

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# Primates are interested in faces



Ferrari et al., PLoS 4(9) e302 (2006)

Video is in public domain courtesy of PLOS Biology.

# Faces elicit automatic emotional, communicative, and cognitive responses

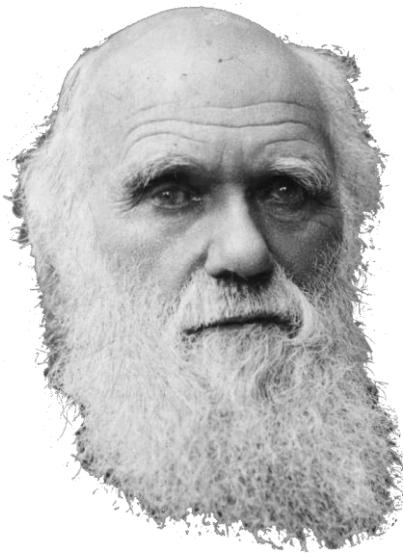


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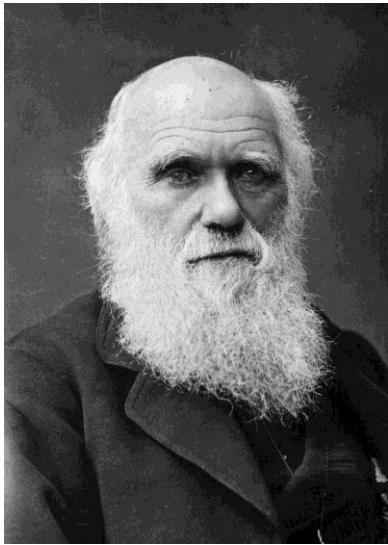
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# **Faces elicit automatic emotional, communicative, and cognitive responses**

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# Social Perception starts with Faces

- gender, age
- personal identity
- trustworthiness, attractiveness (Willis & Todorov, 2007)
- mood, overt direction of attention

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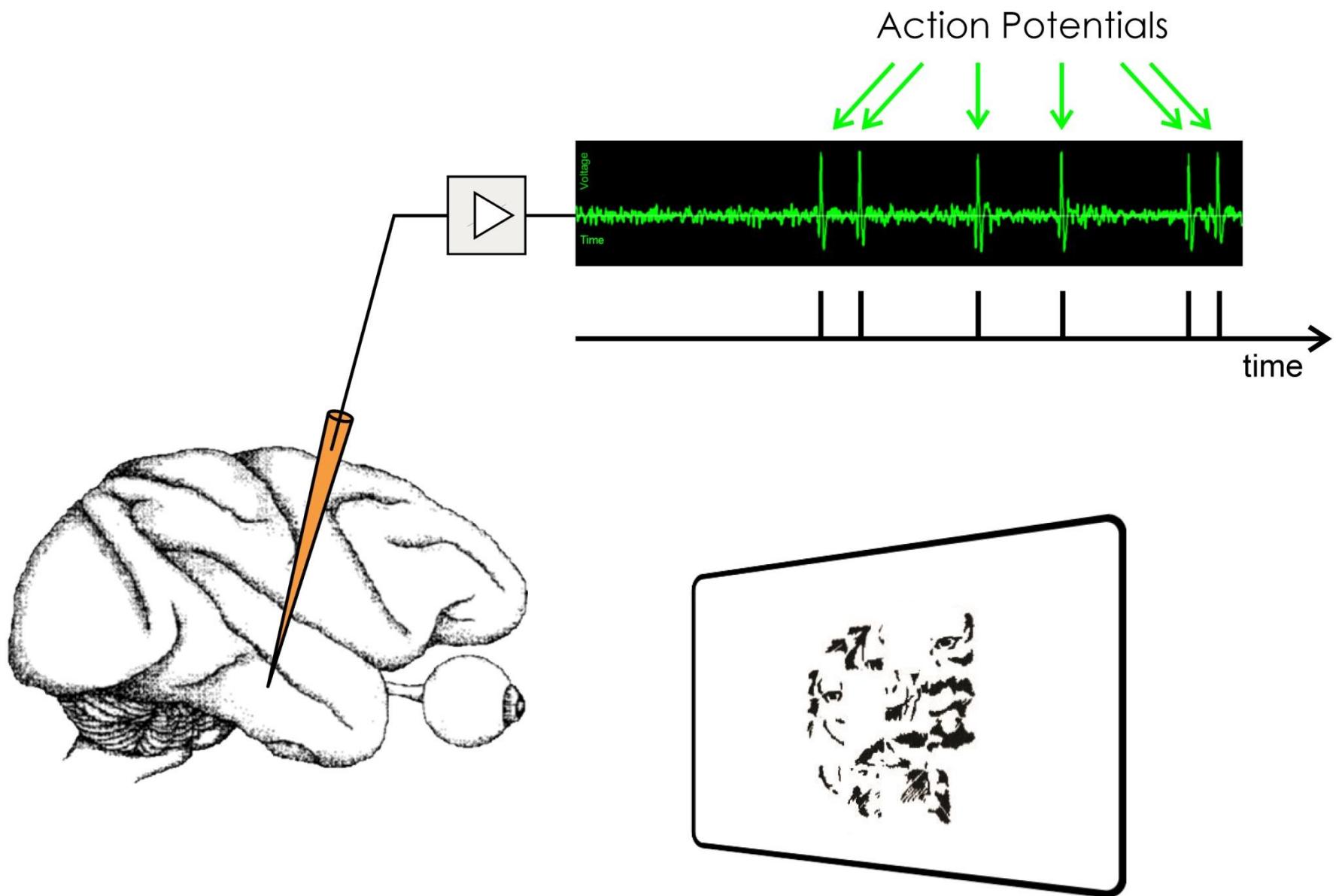


Section of St. Cecilia, Raphael

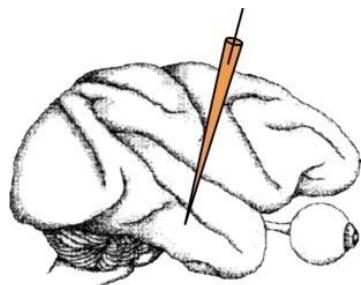
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# The Neural Basis of Face Recognition



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Source: Gross, Charles G. "Single neuron studies of inferior temporal cortex."  
Neuropsychologia 46, no. 3 (2008): 841-852.



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Source: Gross, Charles G. "Single neuron studies of  
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3 (2008): 841-852.



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Please see lecture video or see Figure 4 from Perrett, David Ian, J. K. Hietanen, M. W. Oram, P. J. Benson, and E. T. Rolls. "Organization and functions of cells responsive to faces in the temporal cortex [and discussion]." Philosophical Transactions of the Royal Society of London B: Biological Sciences 335, no. 1273 (1992): 23-30.



Nancy  
Kanwisher

Courtesy of Len Rubenstein.  
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# The Functional Anatomy of Face Recognition

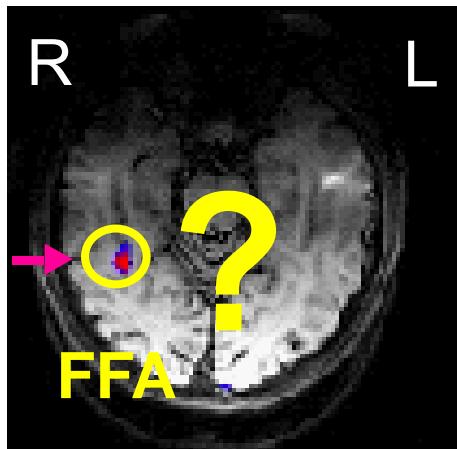
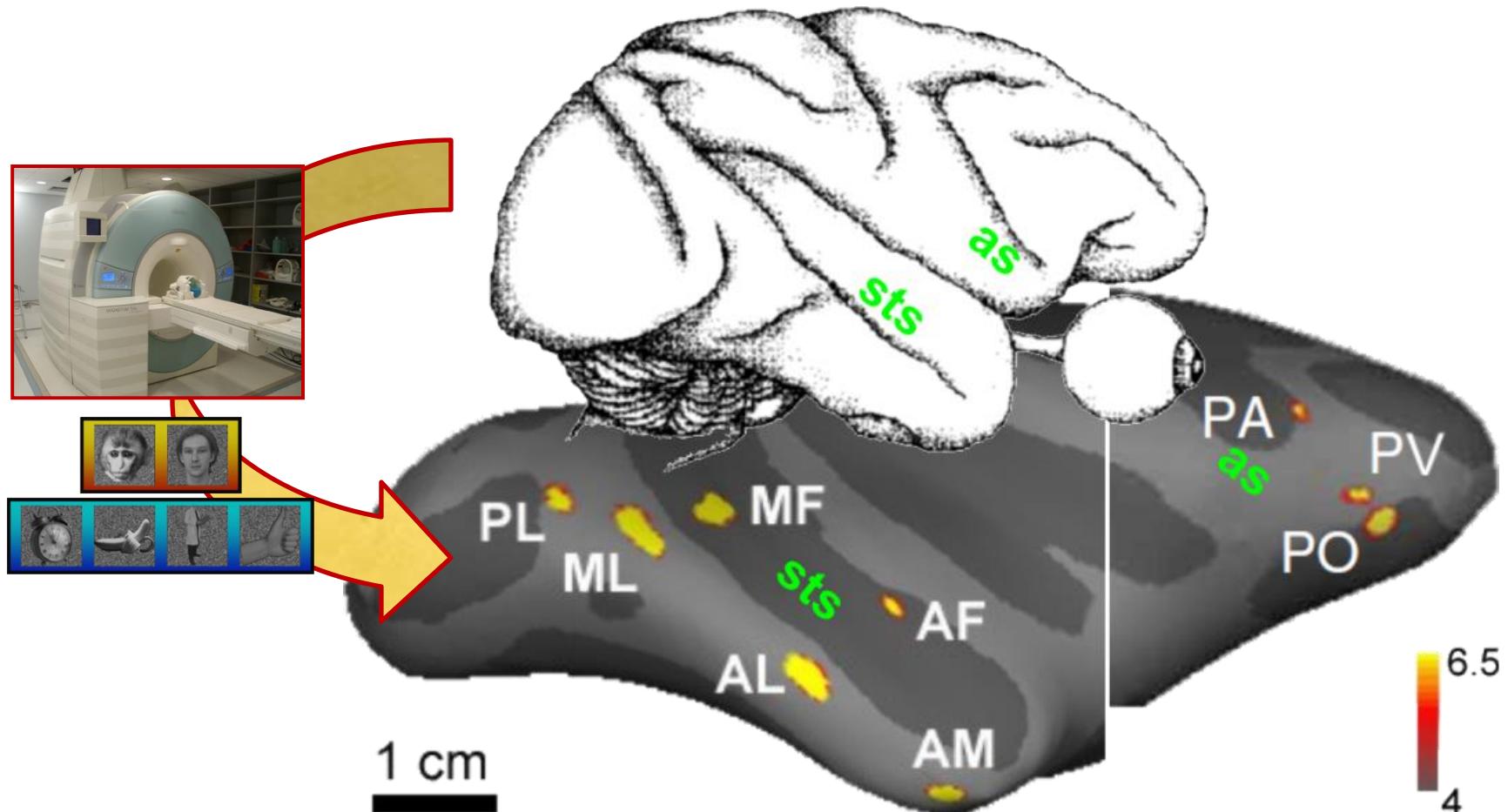


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video.

- Are face areas domain specific modules – or just the tip of the iceberg of face-responsive temporal lobe regions?
- Do monkeys have localized face areas like humans - or not, since electrophysiology seems to suggest broad distribution of face cells across temporal lobe regions?

# The macaque face processing system: composition



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# The Functional Anatomy of Face Recognition

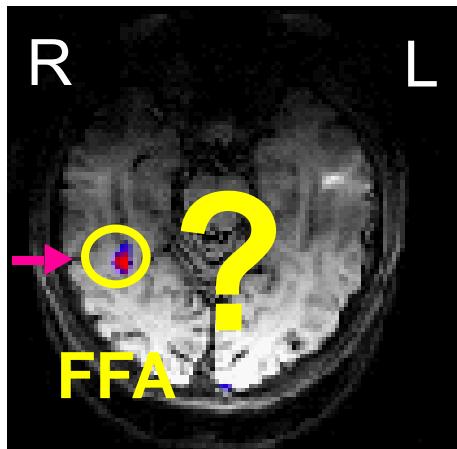
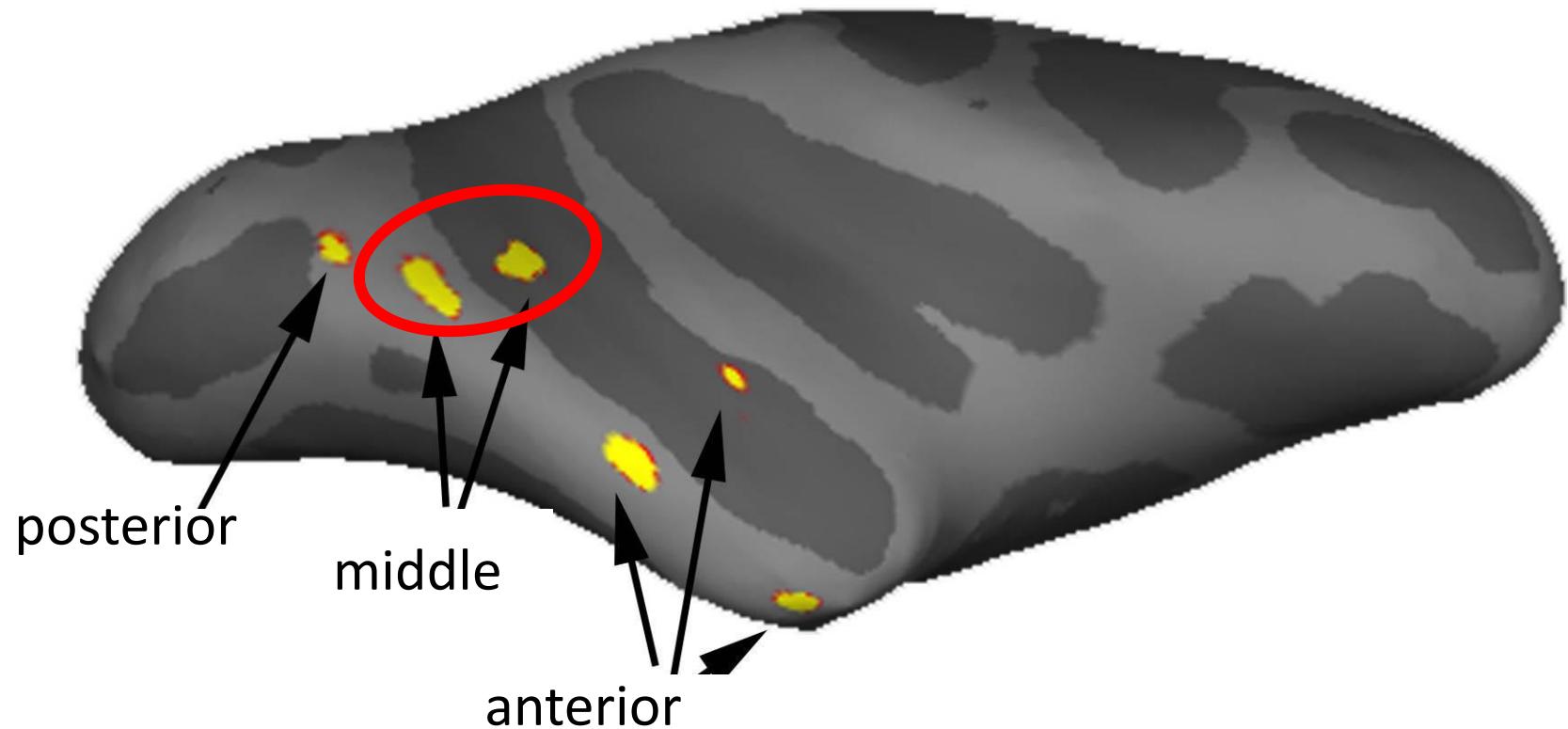


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video.

- Are face areas domain specific modules – or just the tip of the iceberg of face-responsive temporal lobe regions?
- **Monkeys have localized face areas like humans** - or not, since electrophysiology seems to suggest broad distribution of face cells across temporal lobe regions? ✓

# How face-selective are the face patches?

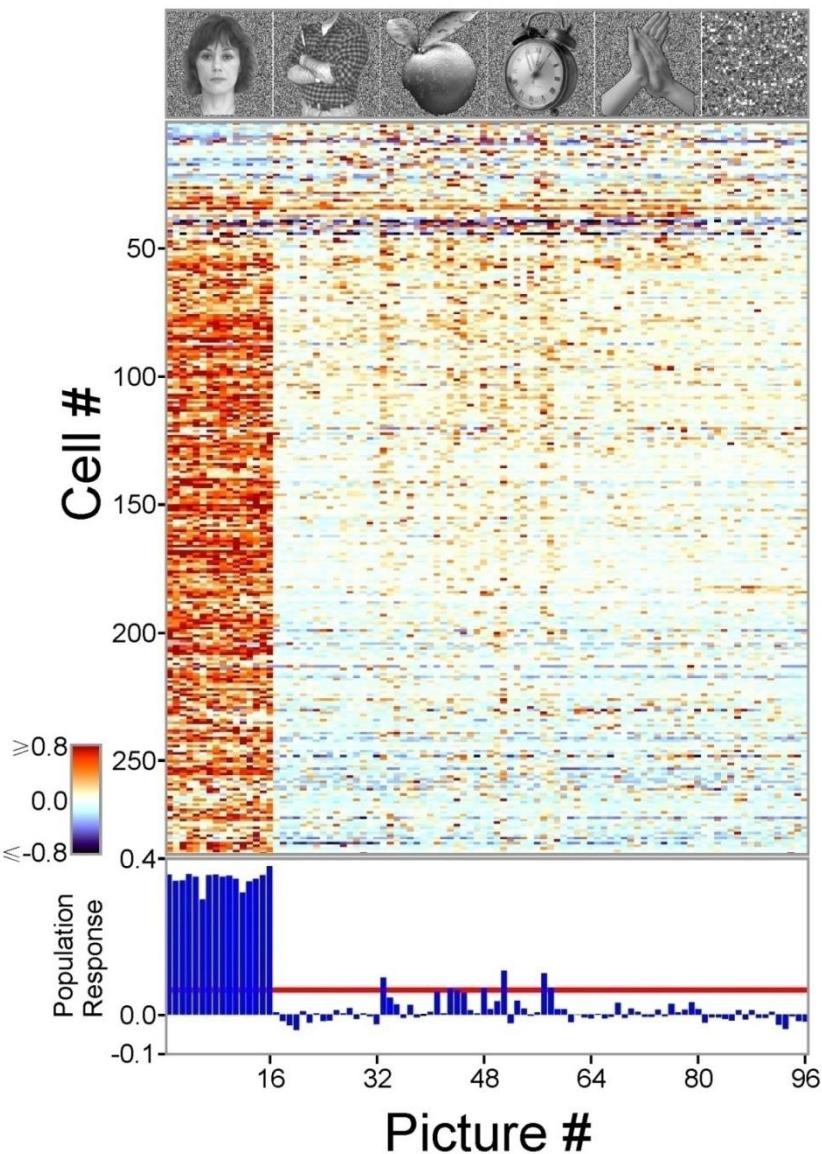




7°

Random order  
200 msec ON, 200 msec OFF  
5-10 repetitions





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Source: Freiwald, Winrich A., Doris Y. Tsao, and Margaret S. Livingstone. "A face feature space in the macaque temporal lobe." *Nature neuroscience* 12, no. 9 (2009): 1187-1196.

# Middle Face Patch Cells

- virtually all are **face selective**
- respond (more weakly) to **non-face objects** that share visual features with faces



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# Face cells, hierarchies, grandmother and gnostic neurons

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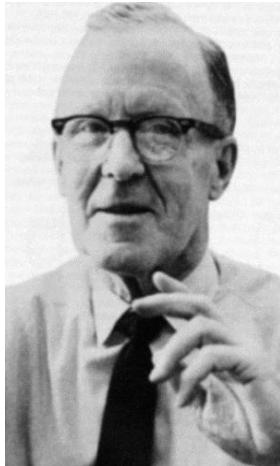
***David Hubel &  
Torsten Wiesel***



***Jerome Lettvin***

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# What is the neural code?



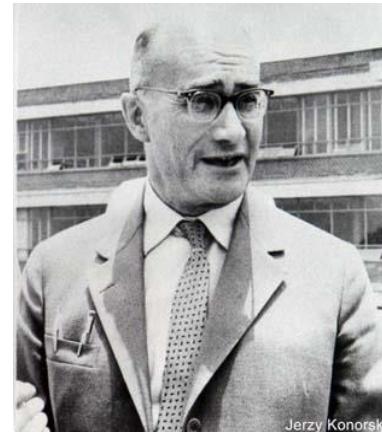
Donald Hebb "cell assembly"



Karl Lashley "mass action"

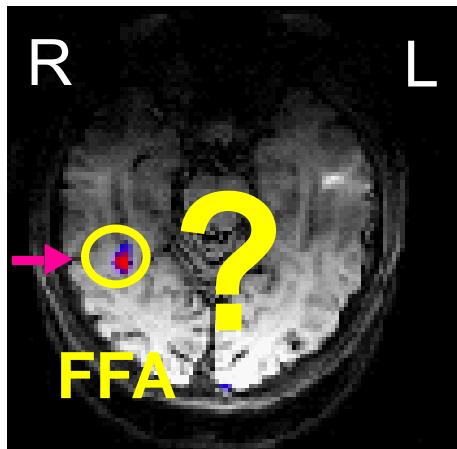


Horace Barlow, "pontifical cell"



*Integrative Activity of the Brain* (1967)  
Jerzy Konorski "gnostic unit"

# The Functional Anatomy of Face Recognition



- Face patches appear to be dedicated domain specific modules – or just the tip of the iceberg of face responsive temporal lobe regions?

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video.

- Monkeys have localized face areas like humans - or not, since electrophysiology seems to suggest broad distribution of face cells across temporal lobe regions?

# Middle Face Patch Cells

- ... are virtually all **face selective**

## Practical Implications

- We have **unprecedented access** to functionally **homogenous populations** of cells coding for **one high-level object category**
- We can **causally** test the role of face-patches for face processing



# The macaque face processing system: causal role in face detection

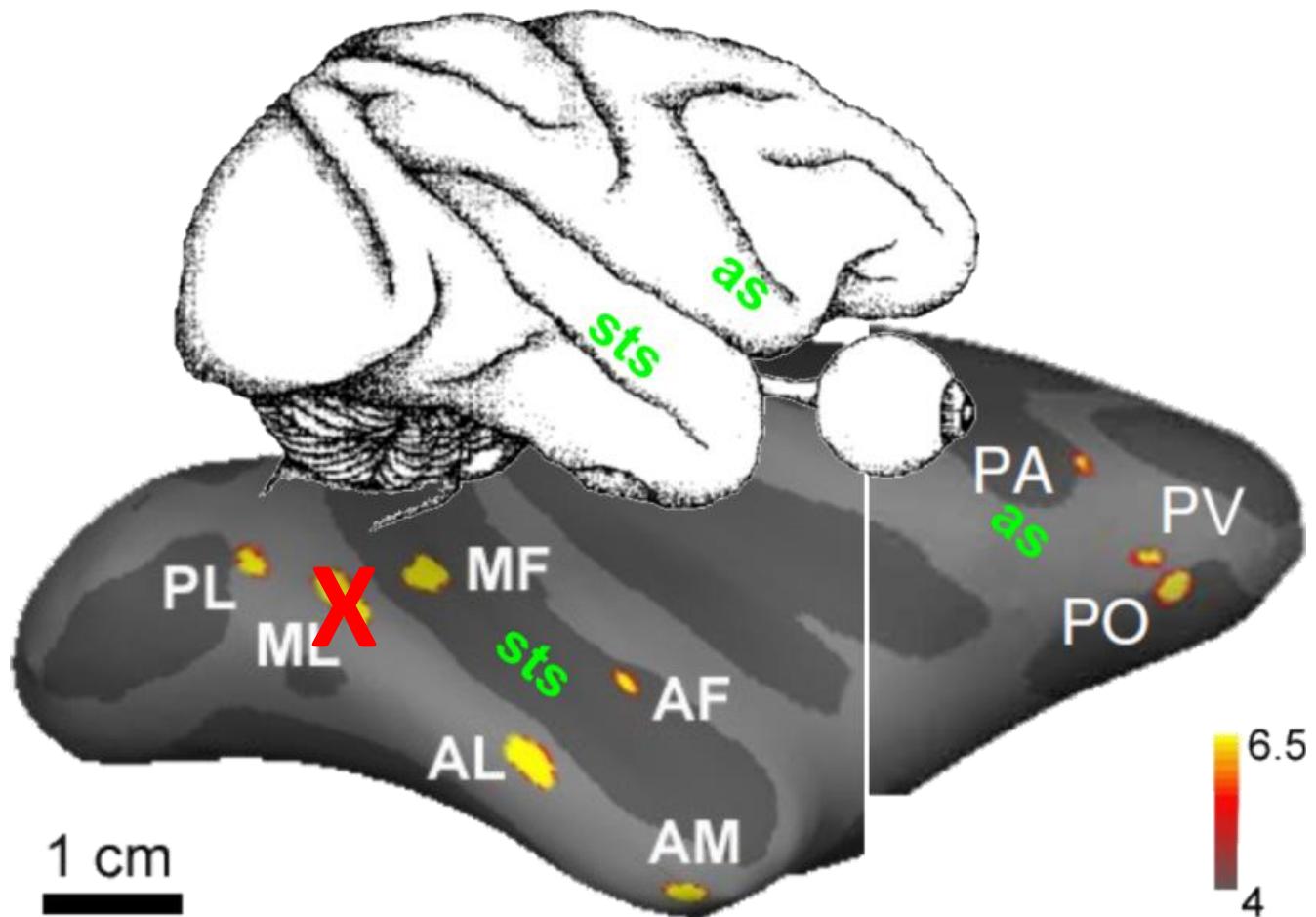
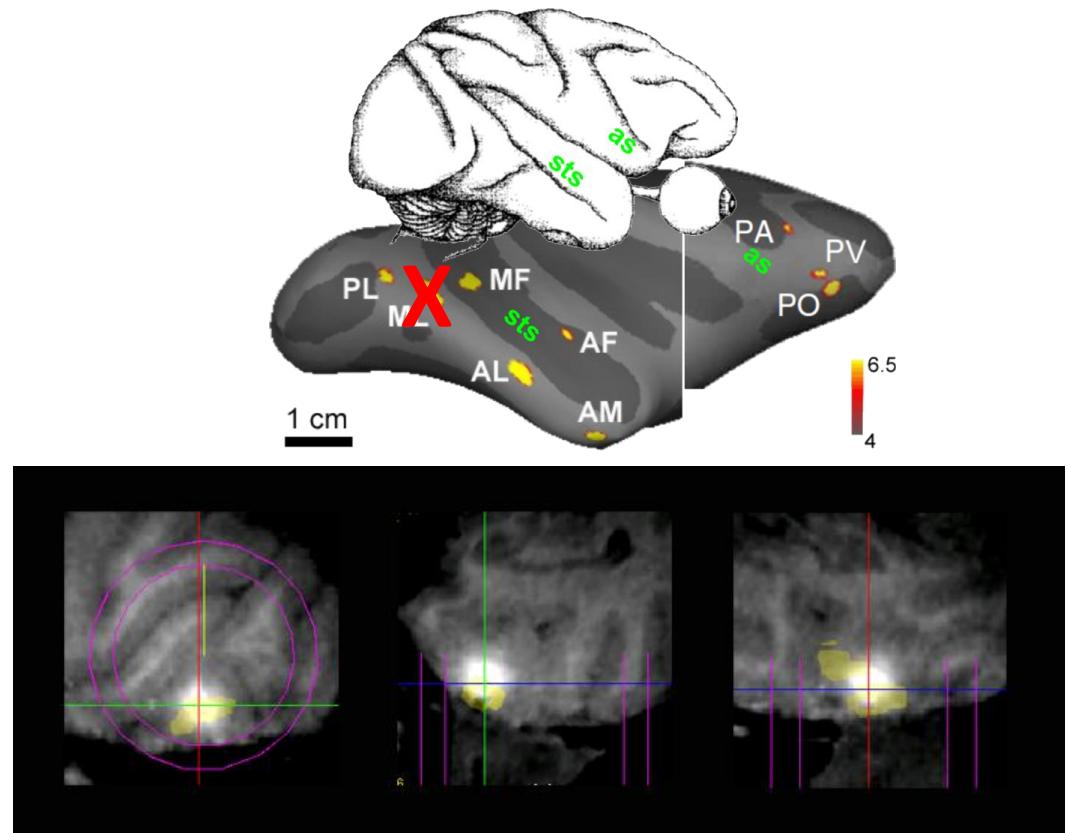
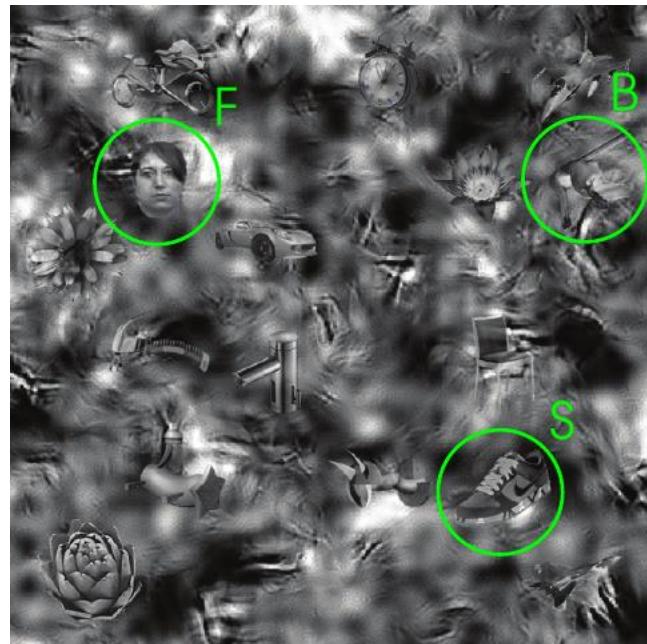
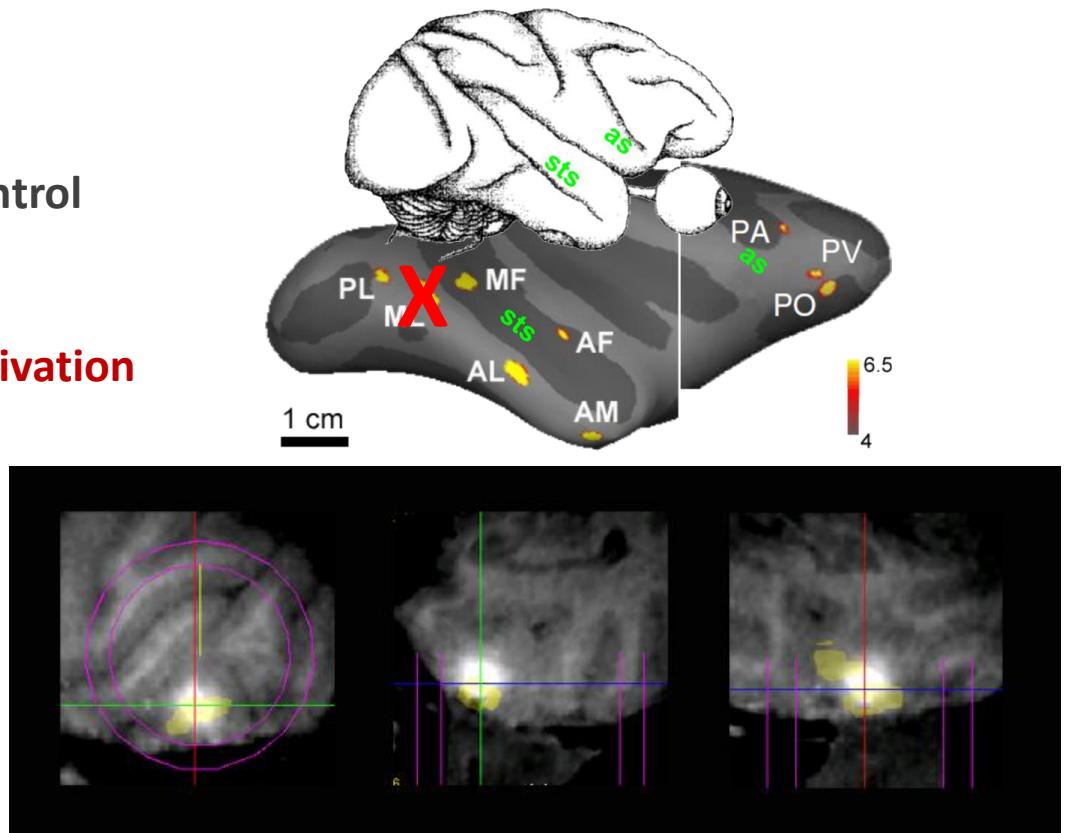
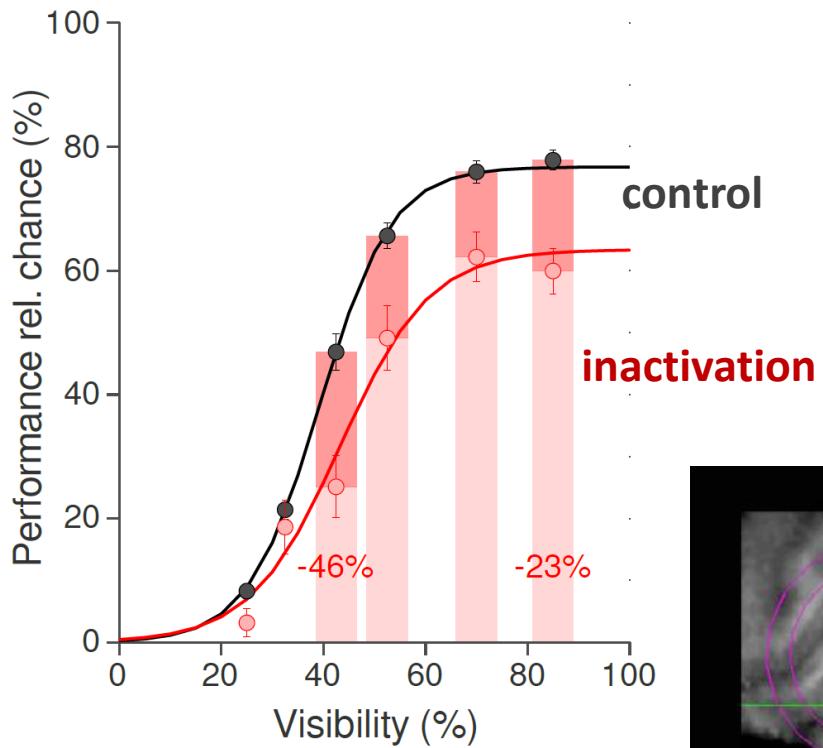


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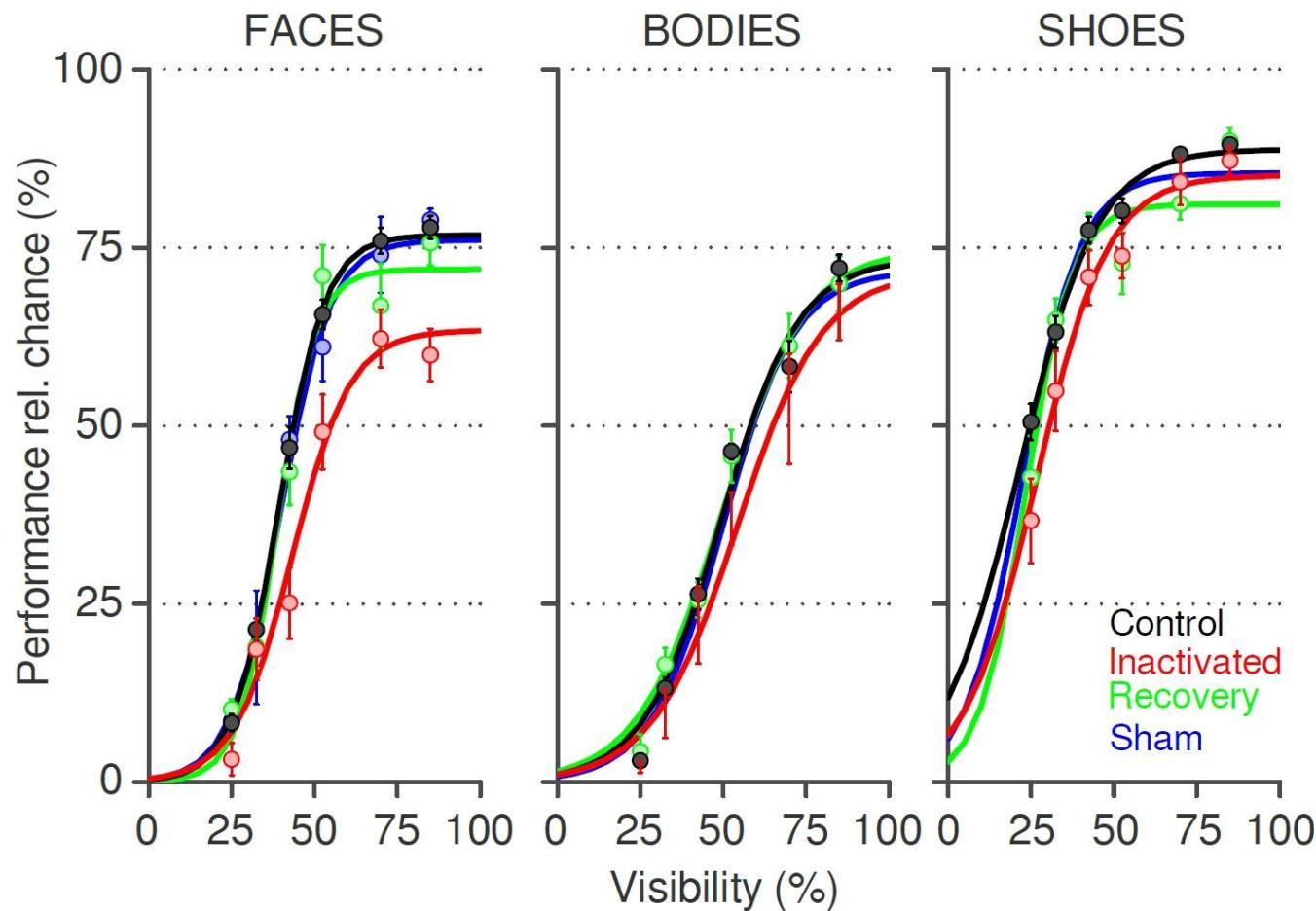
# The macaque face processing system: causal role in face detection

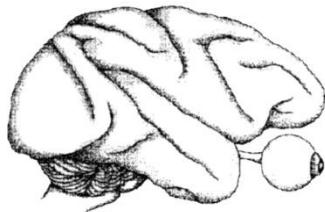


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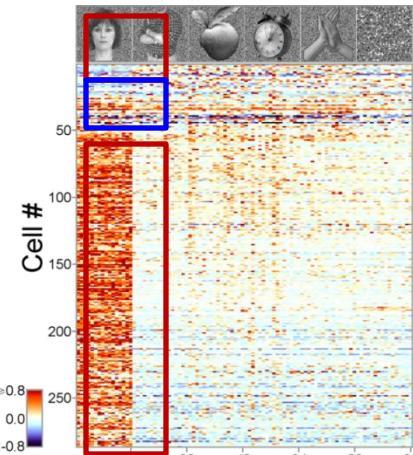


# The macaque face processing system: causal role in face detection

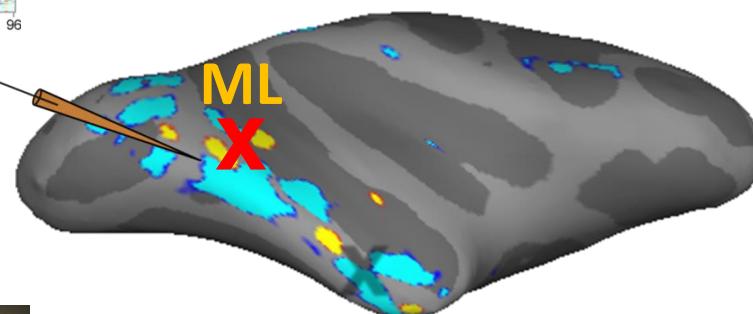
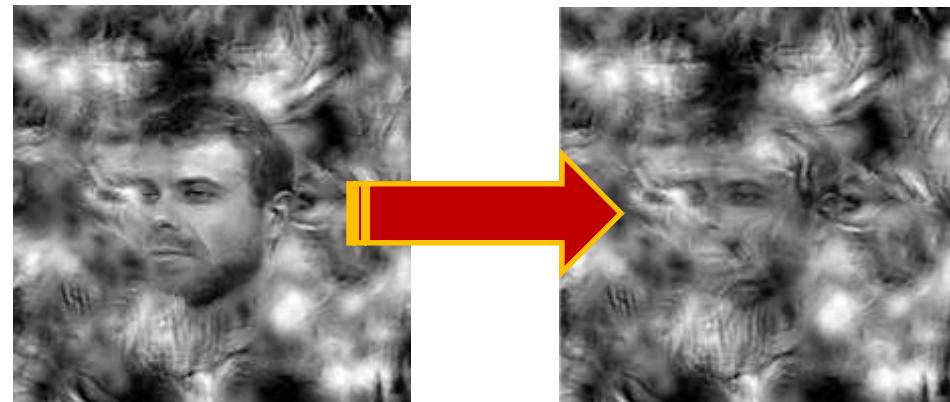


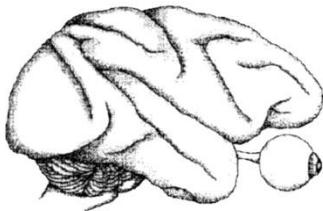


# The macaque face processing system: face-domain specific modularity

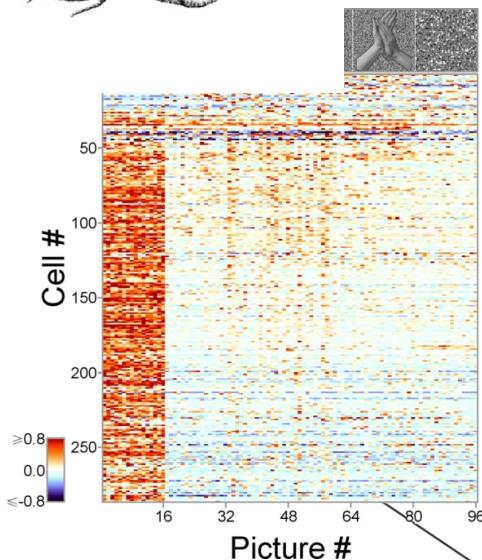


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Source: Freiwald, Winrich A., Doris Y. Tsao, and Margaret S. Livingstone  
"A face feature space in the macaque temporal lobe." *Nature neuroscience* 12, no. 9 (2009): 1187-1196.



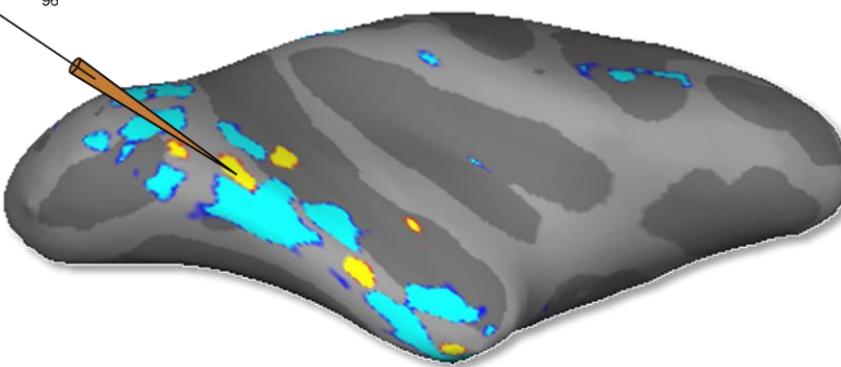


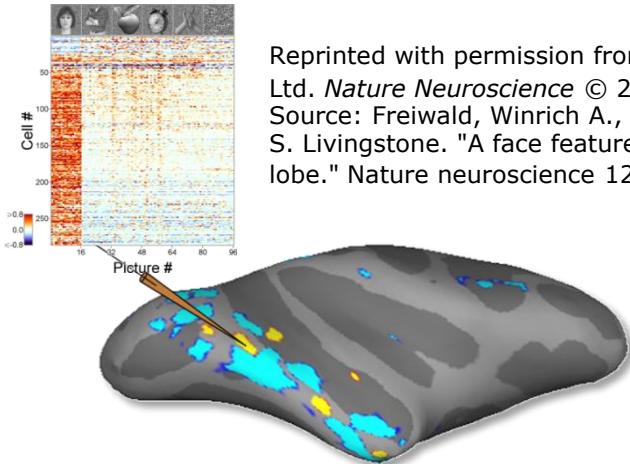
# The macaque face processing system



We have **unprecedented access** to functionally **homogenous populations** of cells coding for **one high-level object category**

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Source: Freiwald, Winrich A., Doris Y. Tsao, and Margaret S. Livingstone  
"A face feature space in the macaque temporal lobe." *Nature neuroscience* 12, no. 9 (2009): 1187-1196.

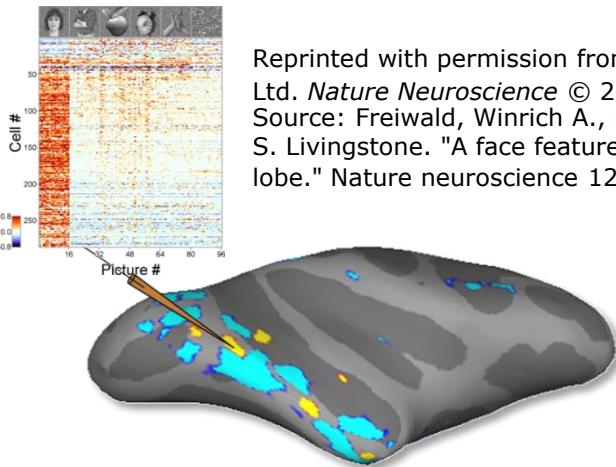




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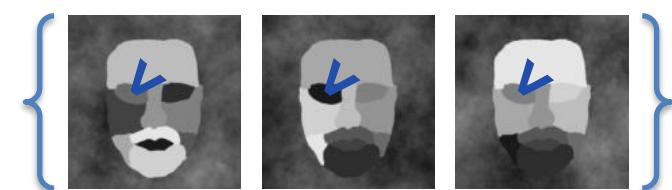
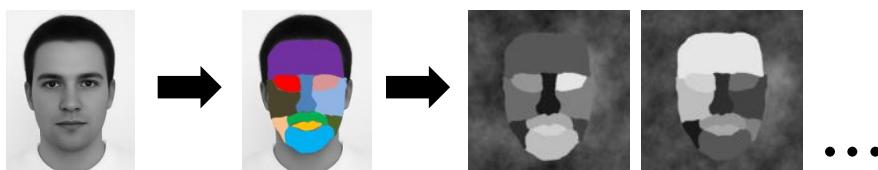
Source: Freiwald, Winrich A., Doris Y. Tsao, and Margaret S. Livingstone. "A face feature space in the macaque temporal lobe." *Nature neuroscience* 12, no. 9 (2009): 1187-1196.



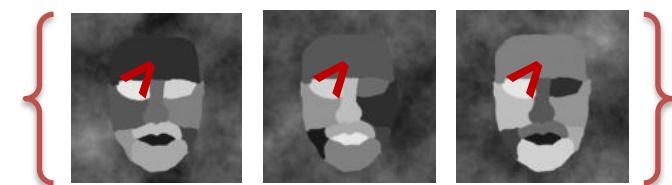
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Source: Freiwald, Winrich A., Doris Y. Tsao, and Margaret S. Livingstone. "A face feature space in the macaque temporal lobe." *Nature neuroscience* 12, no. 9 (2009): 1187-1196.

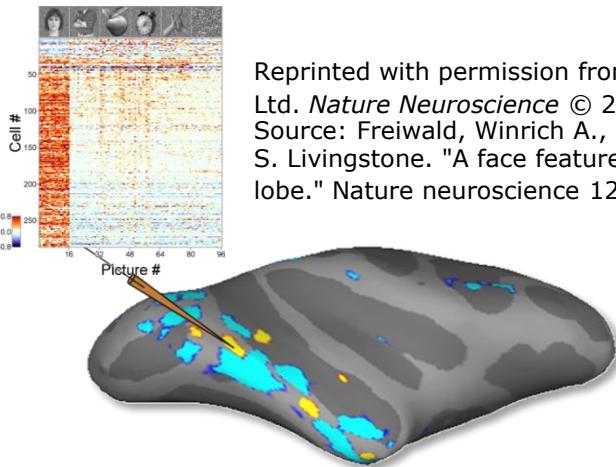
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## Human Psychophysics



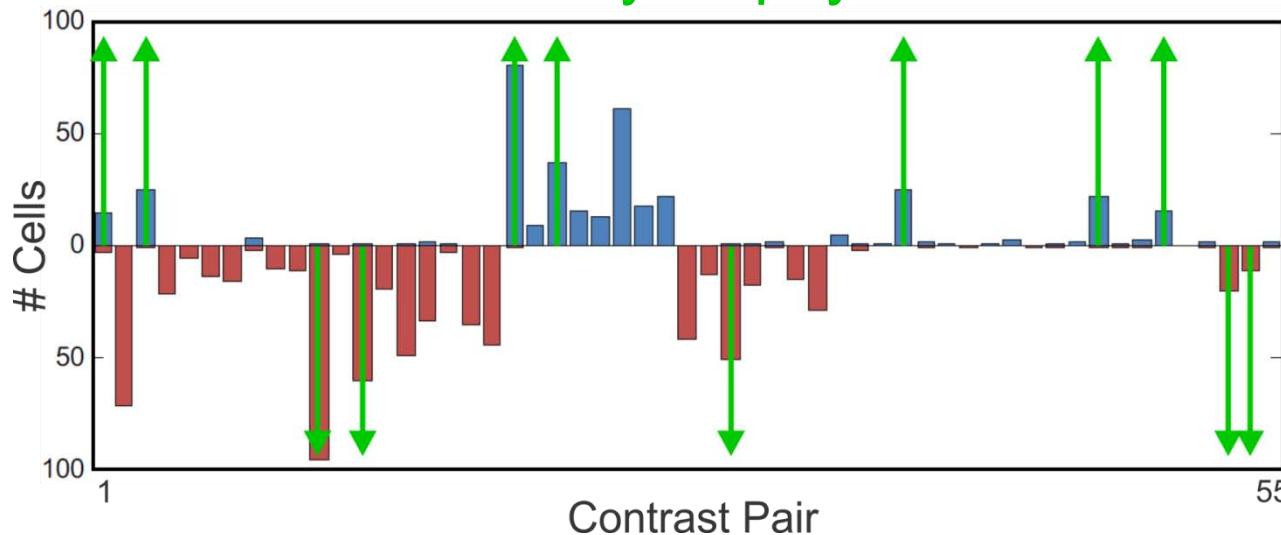
**vs.**



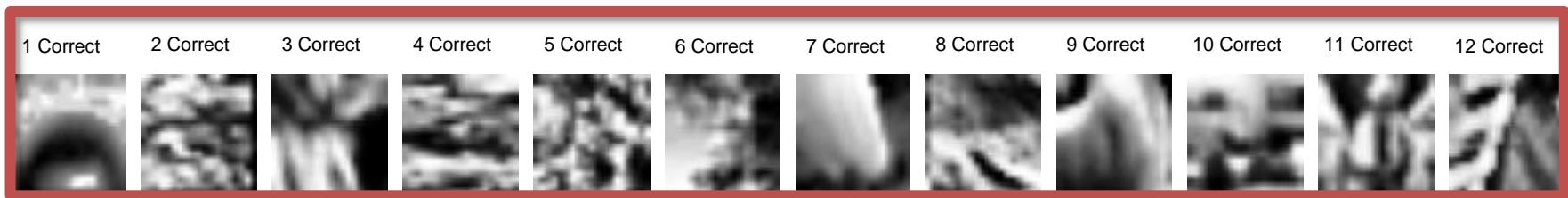
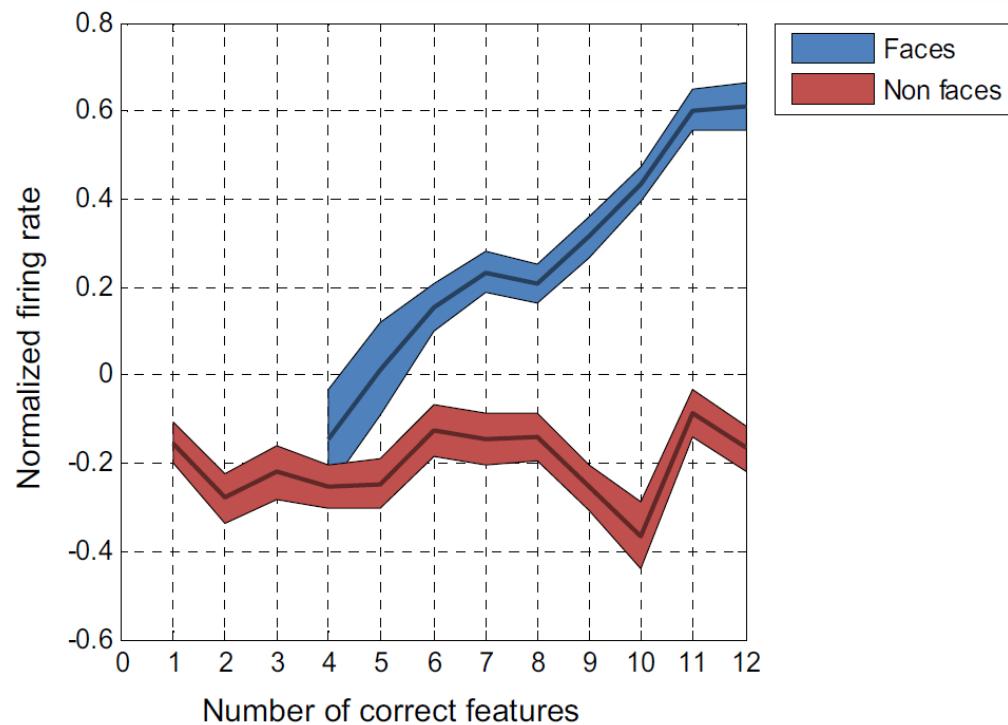
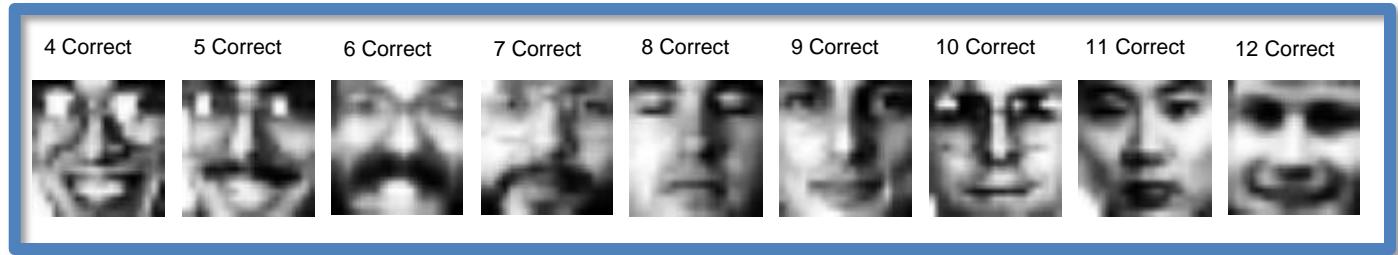


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## Human Psychophysics

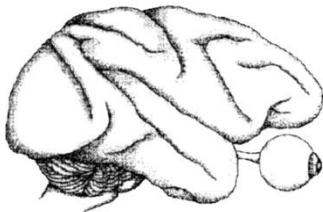


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Source: Ohayon, Shay, Winrich A. Freiwald, and Doris Y. Tsao. "What makes a cell face selective? The importance of contrast." *Neuron* 74, no. 3 (2012): 567-581.

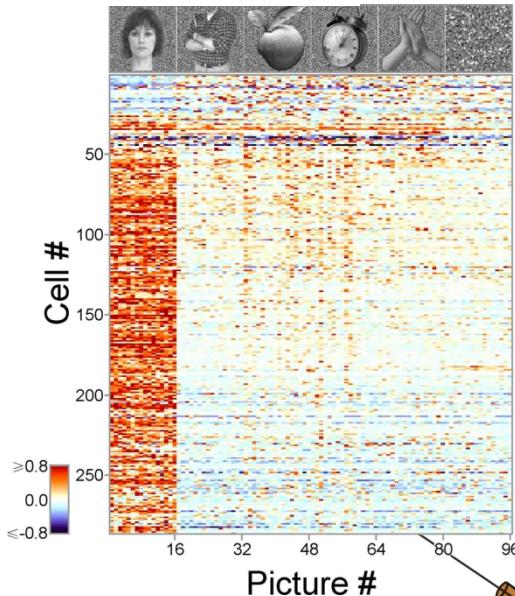


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Source: Ohayon, Shay, Winrich A. Freiwald, and Doris Y. Tsao. "What makes a cell face selective? The importance of contrast." *Neuron* 74, no. 3 (2012): 567-581.

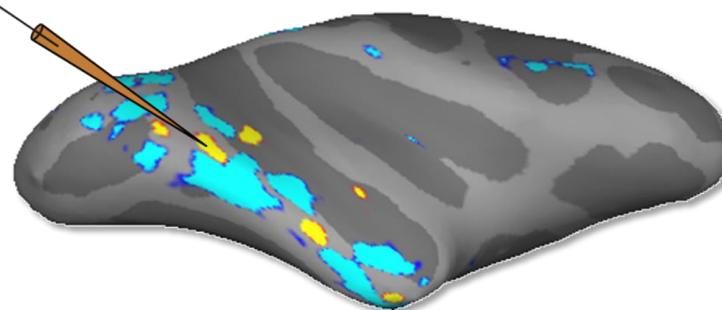


# The macaque face processing system: The Part and the Whole

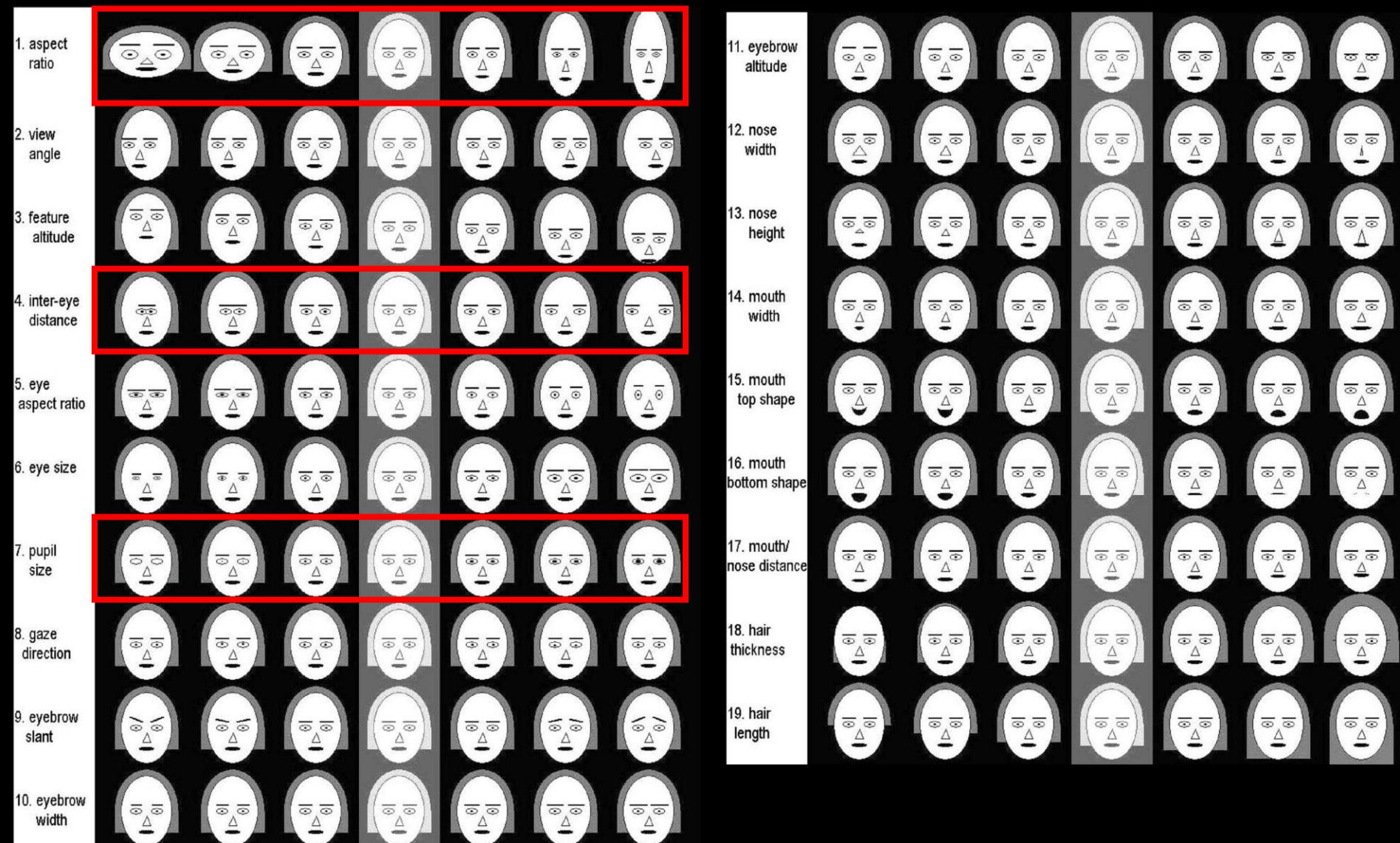


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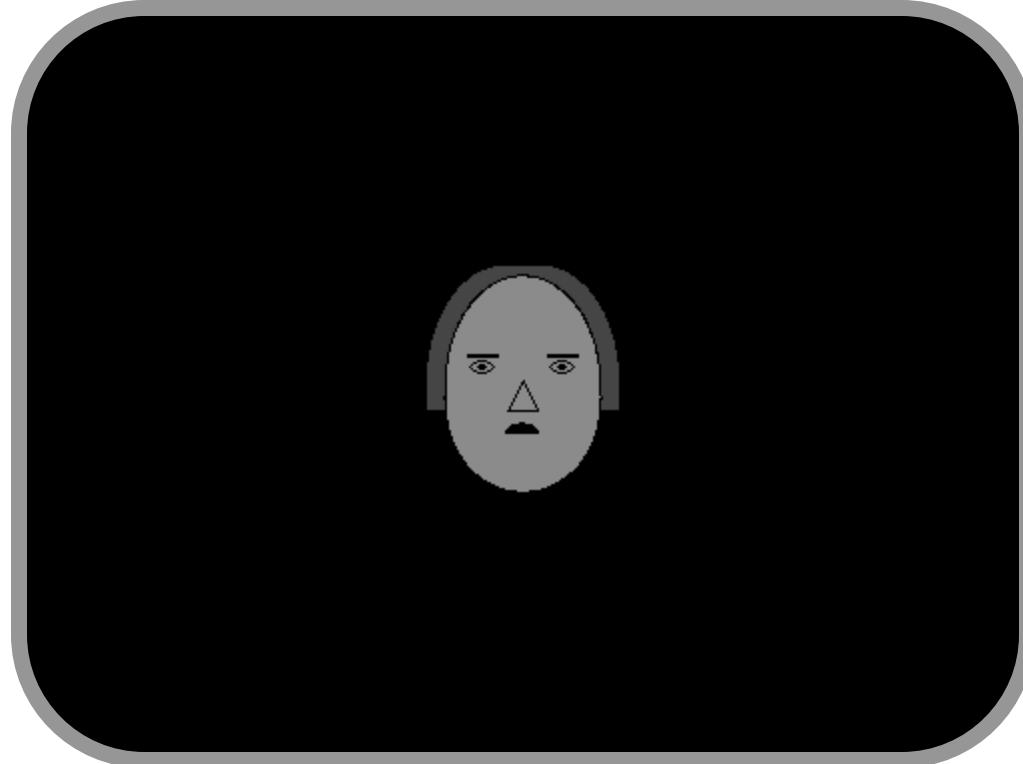


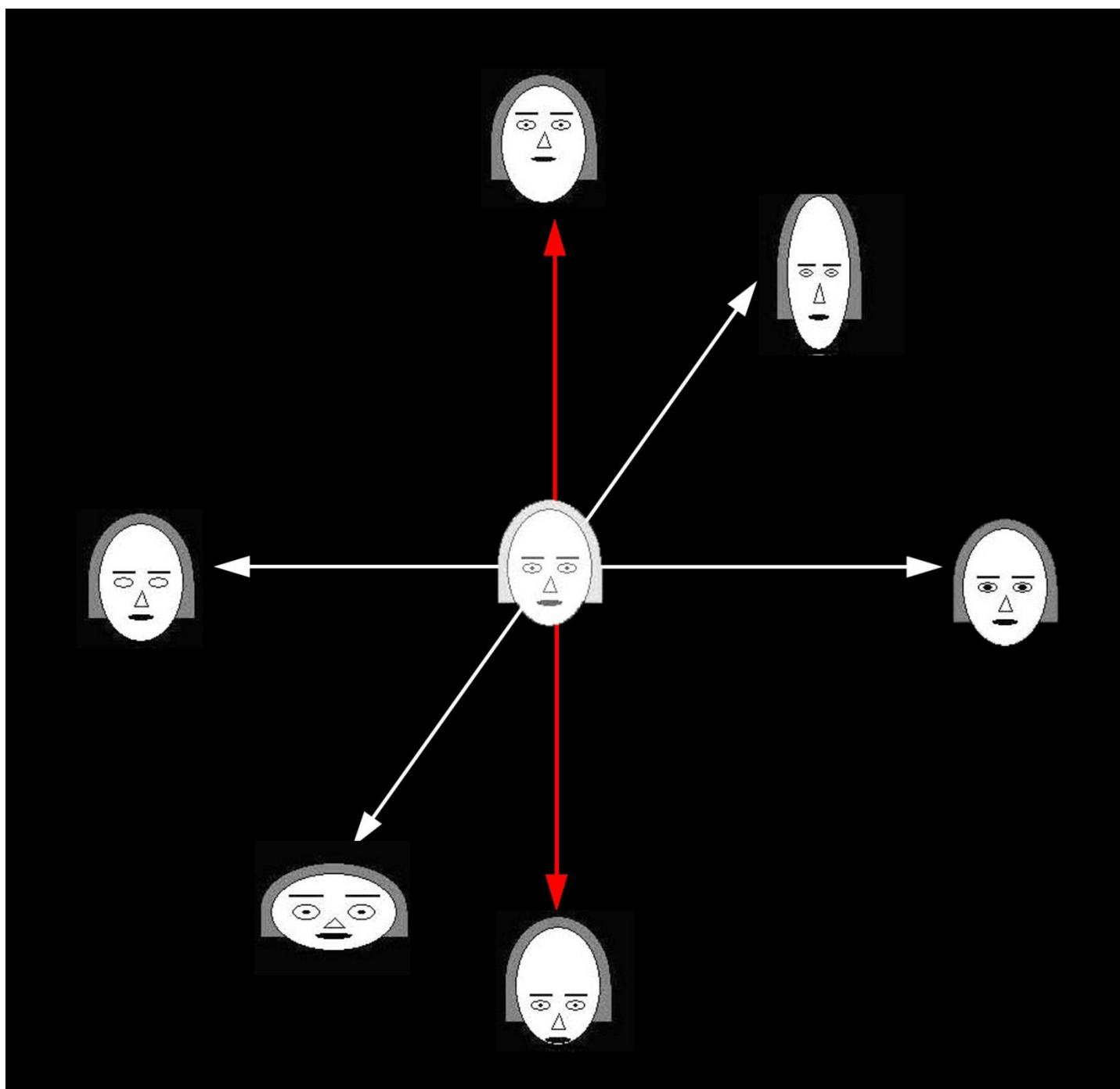
# A Parameterized Cartoon Face Space



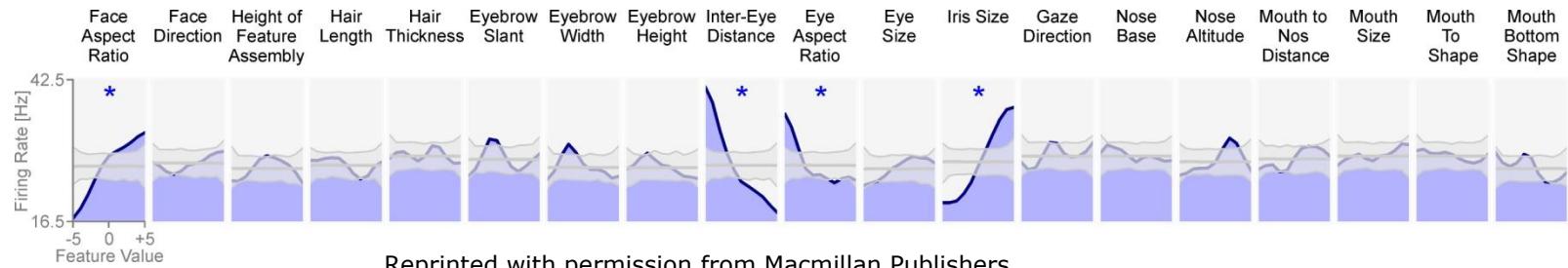
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Source: Freiwald, Winrich A., Doris Y. Tsao, and Margaret S. Livingstone. "A face feature  
space in the macaque temporal lobe." *Nature neuroscience* 12, no. 9 (2009): 1187-1196.

# A Parameterized Cartoon Face Space

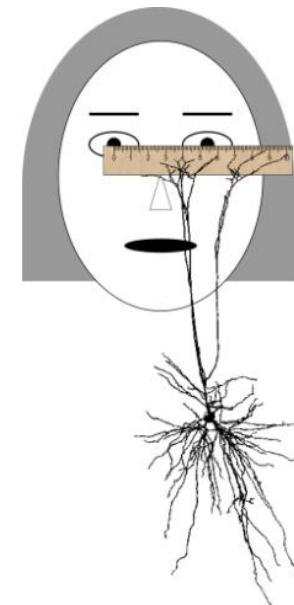
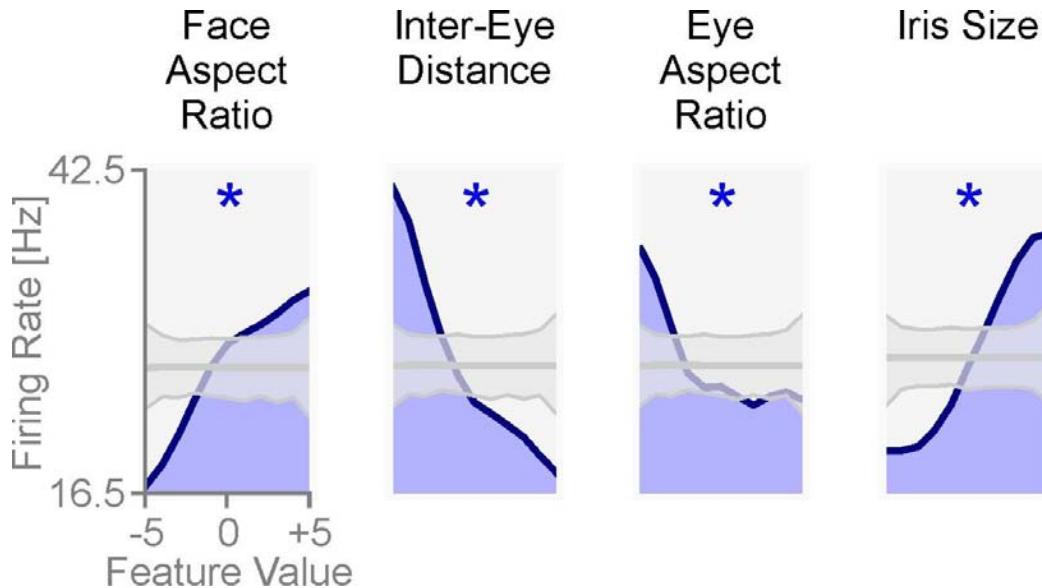




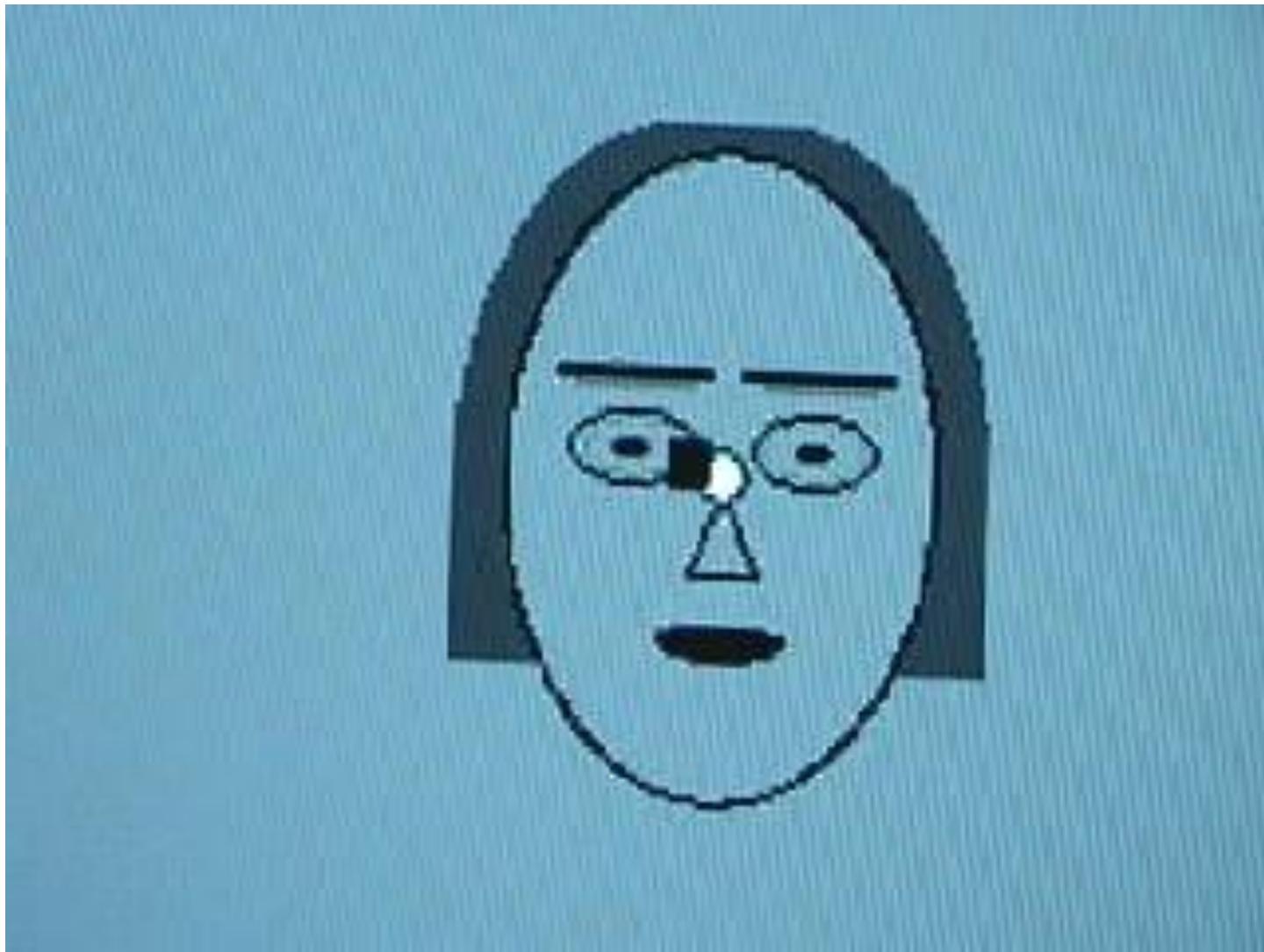
# Tuning to Features: an Example Face Cell



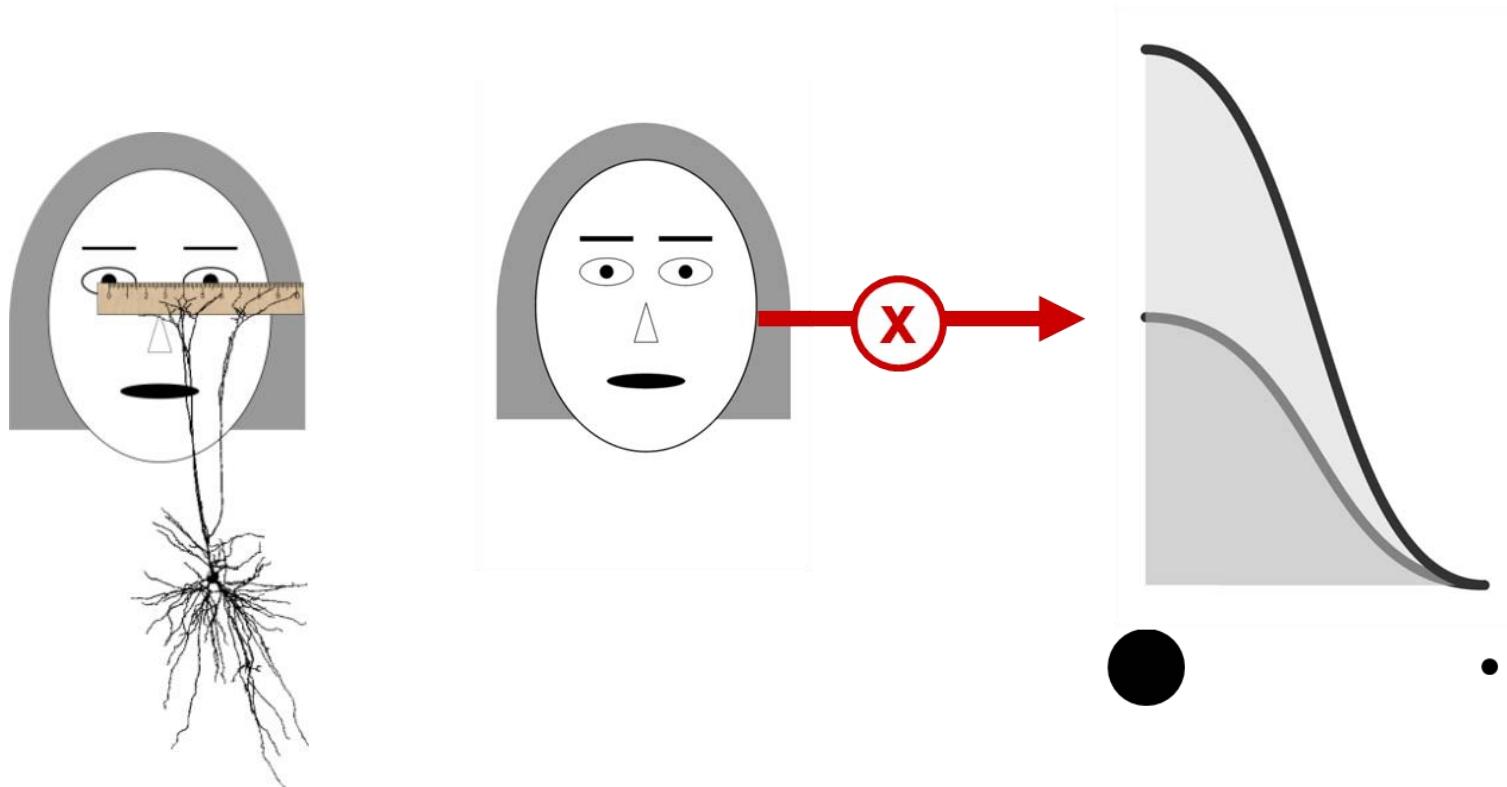
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S. Livingstone. "A face feature space in the macaque temporal  
lobe." *Nature neuroscience* 12, no. 9 (2009): 1187-1196.

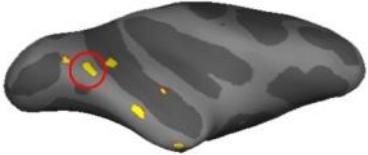


# Are features tuned in isolation?



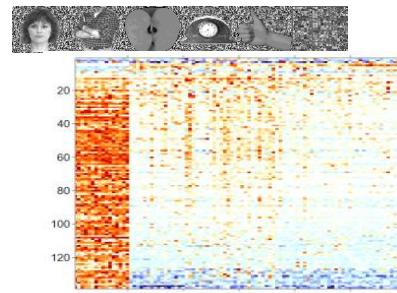
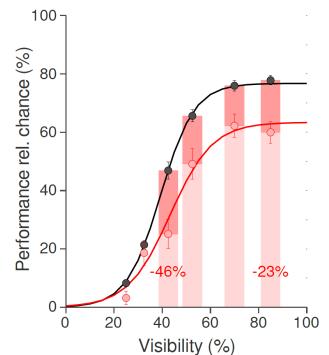
# Feature Tuning & Holistic Gain Modulation in the middle face patches



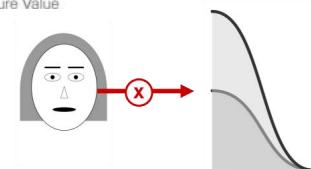
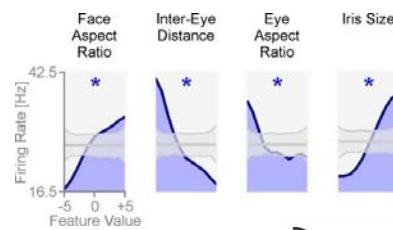


# Middle Face Patches

- Are causally and selectively relevant for face detection
- Cells are virtually all face selective → modules
- Middle face patch neurons are tuned to facial features: thus they care for details
- Gain of tuning curves is modulated by the presence of the entire face: thus middle face patch neurons have holistic coding properties
- They detect qualitative contrast ratios, preferring polarity in much the same way as predicted by computational and psychophysical results.
- We can get a mechanistic understanding of face-recognition
- Thus at the level of the middle face patches, some of the requirements of a face recognition system are met: mechanisms for face detection, encoding of facial features and, encoding of configurations



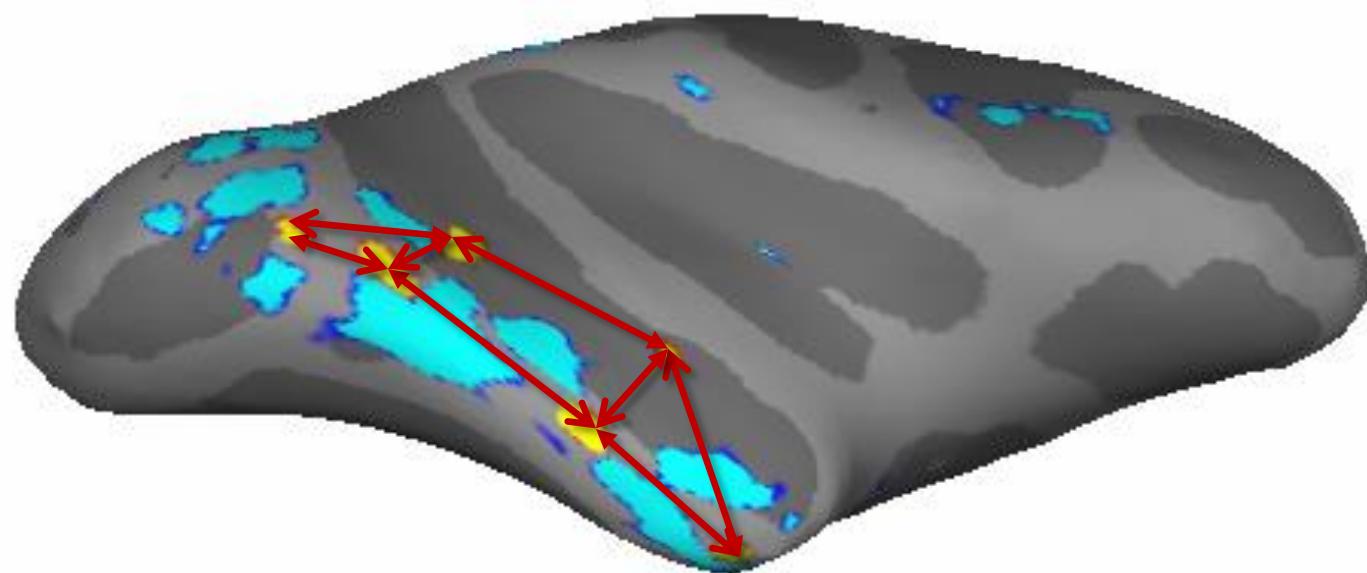
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Source: Freiwald, Winrich A., Doris Y. Tsao, and Margaret S. Livingstone. "A face feature space in the macaque temporal lobe." *Nature neuroscience* 12, no. 9 (2009): 1187-1196.





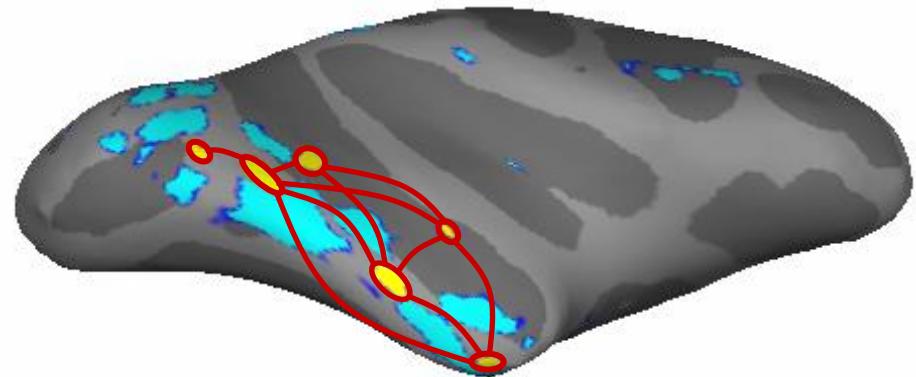
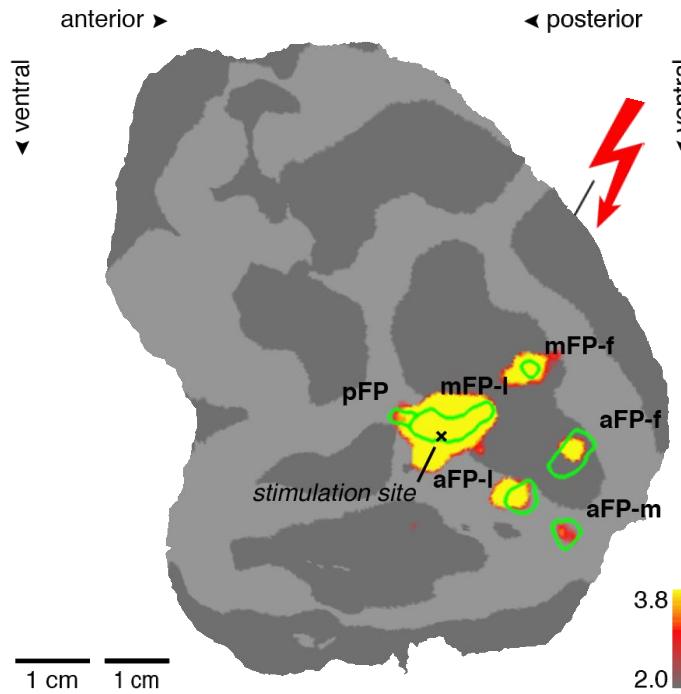
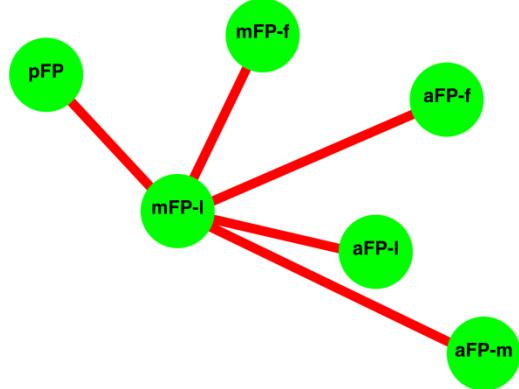
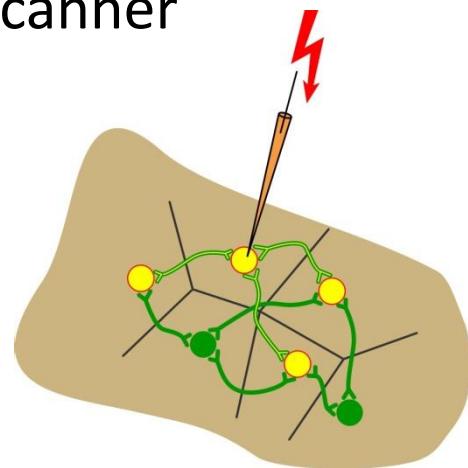
# The macaque face processing system: determining connectivity

Sebastian Möller

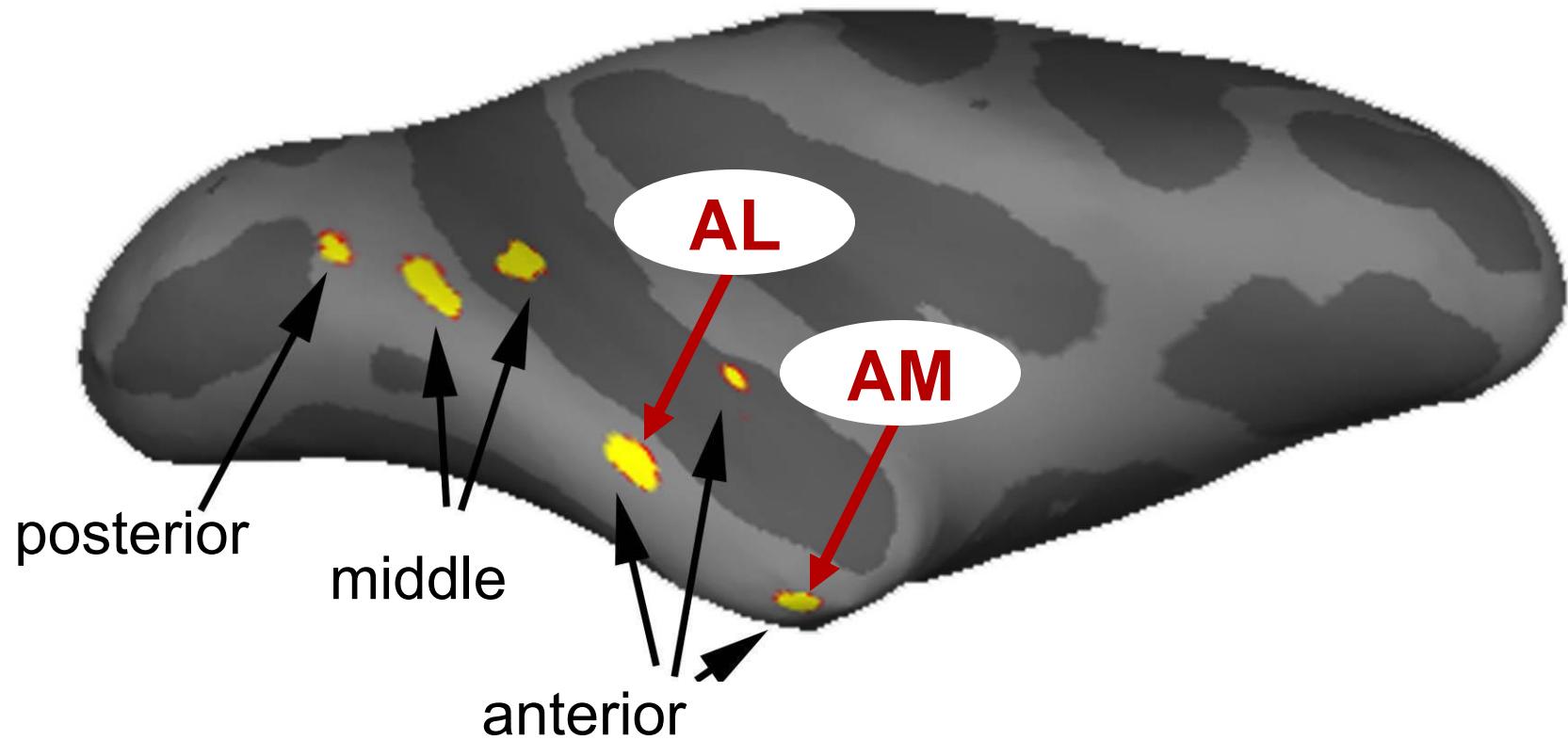


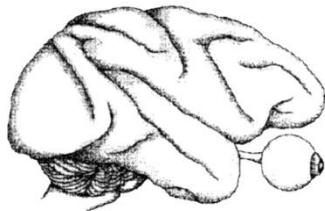
# The macaque face processing system: determining connectivity

electrical stimulation inside  
the MR scanner

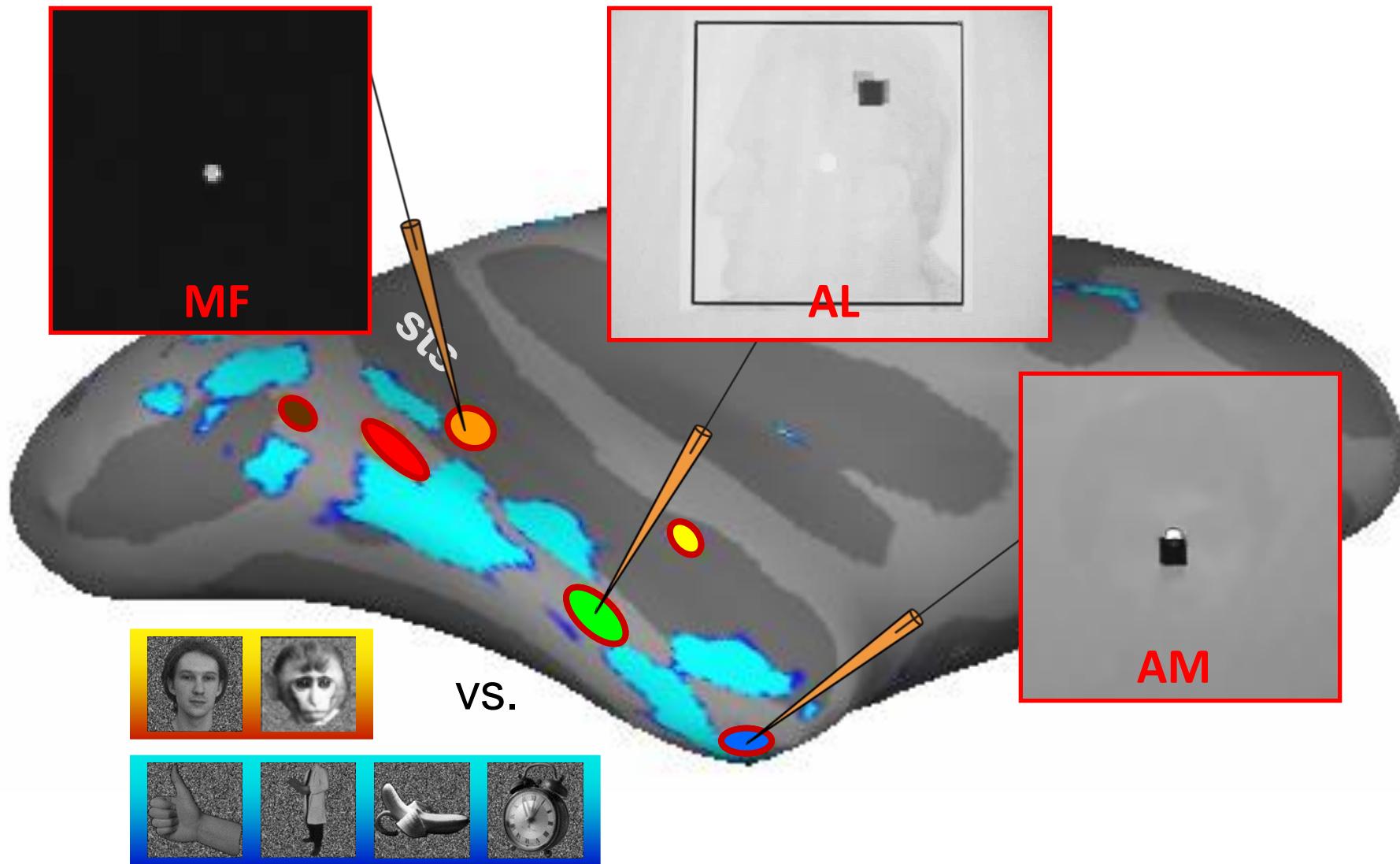


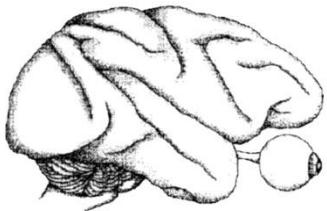
# How does face selectivity develop along the face patch hierarchy?





# Electrophysiological Recordings in Three Face Patches





# The macaque face processing system: why is it organized the way it is?

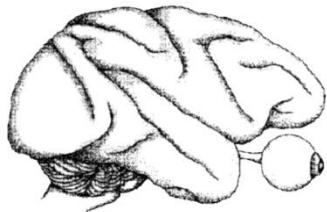
Affine Transformations



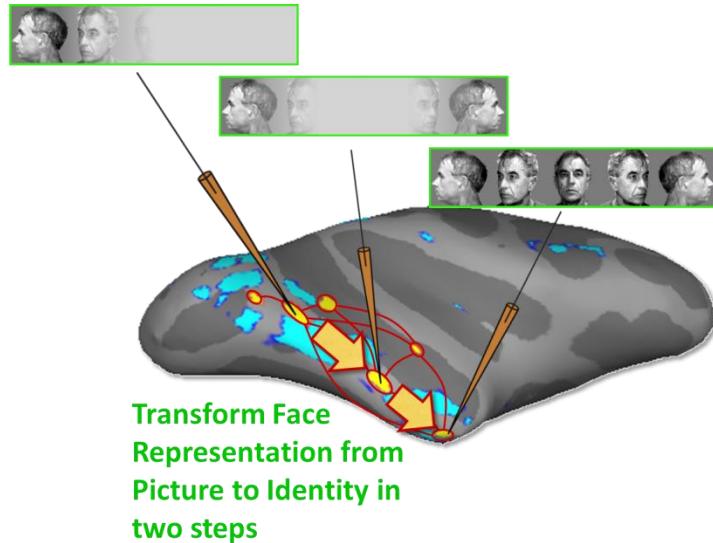
Non-affine Transformations



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# The macaque face processing system: why is it organized the way it is?

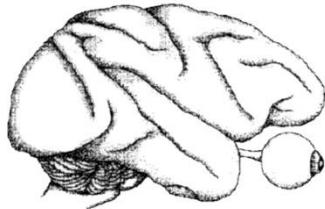


**Modular Architecture**  
**3-Level Processing Hierarchy**

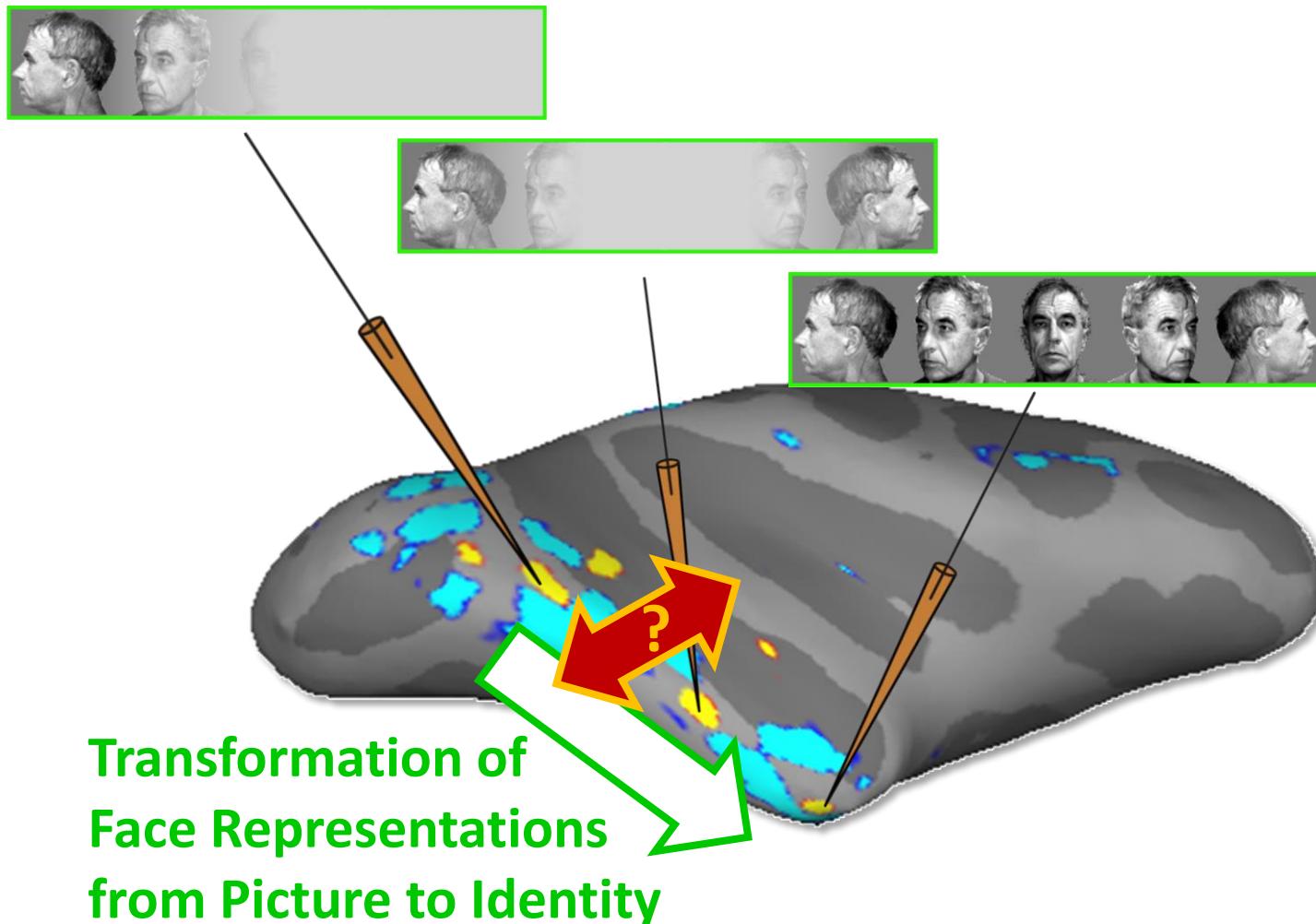
**Level 1: Face Filter**  
**Level 3: Identification**  
**+ Hebbian Learning Rule**

=

**Level 3: Invariance**  
**Level 2: Mirror-Symmetry**



# The macaque face processing system: transformations



# from Faces to Agents

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Please see lecture video or Figure 3 from Looser, Christine E., and Thalia Wheatley. "The tipping point of animacy how, when, and where we perceive life in a face." *Psychological science* 21, no. 12 (2010): 1854-1862.

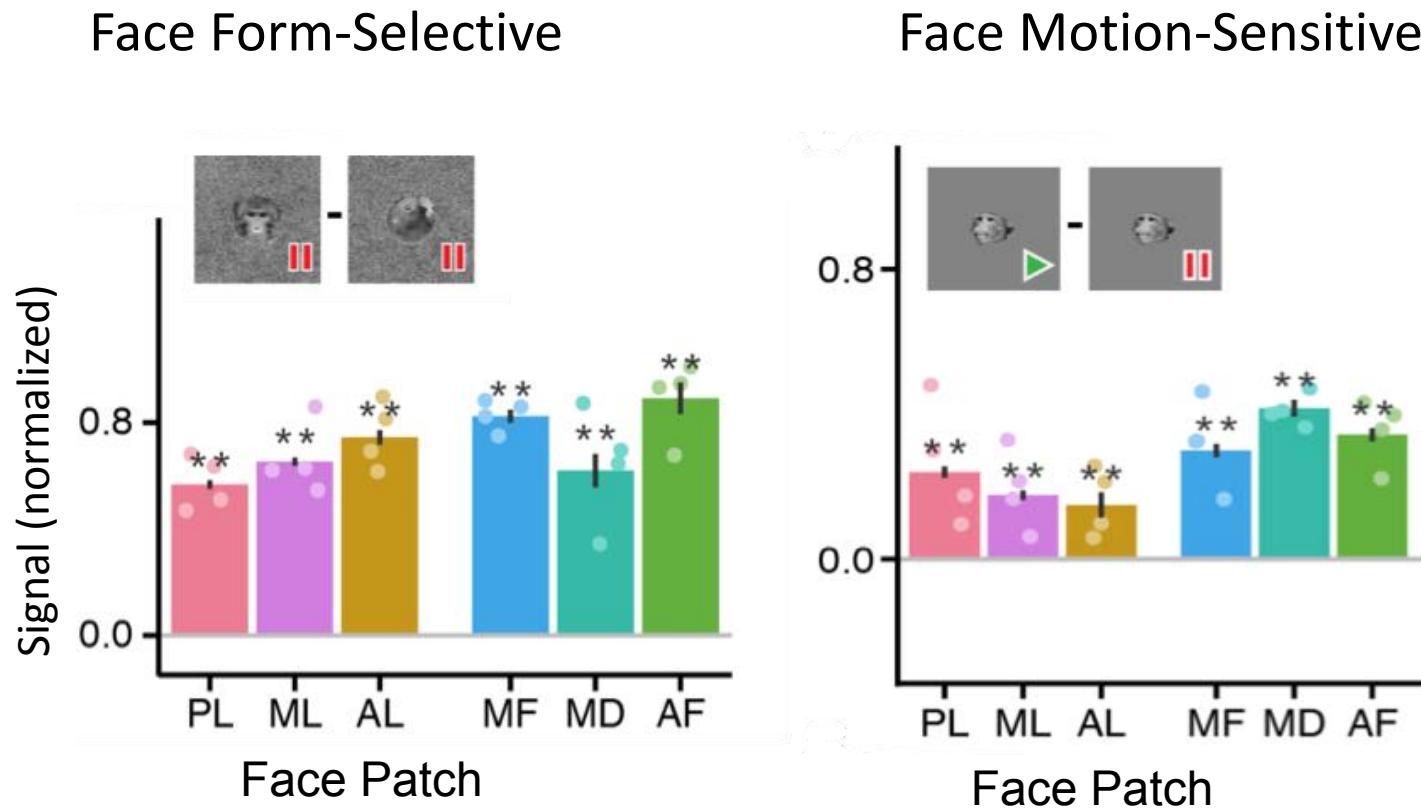
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# **The macaque face processing system: sensitivity to stimulus motion**



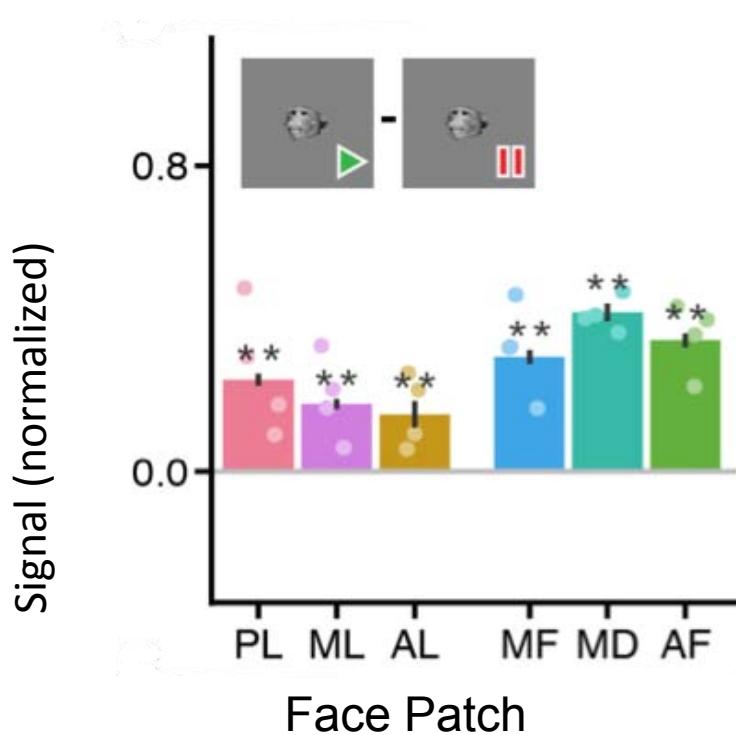
# The macaque face processing system: Sensitivity to stimulus motion



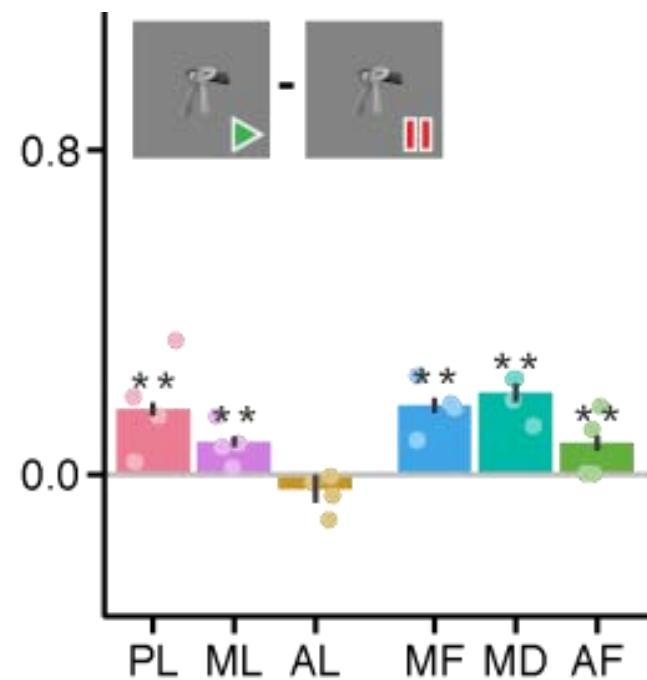
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Source: Fisher, Clark, and Winrich A. Freiwald. "Contrasting specializations for facial motion  
within the macaque face-processing system." *Current Biology* 25, no. 2 (2015): 261-266.

# The macaque face processing system: Sensitivity to stimulus motion

Face MotionSensitive



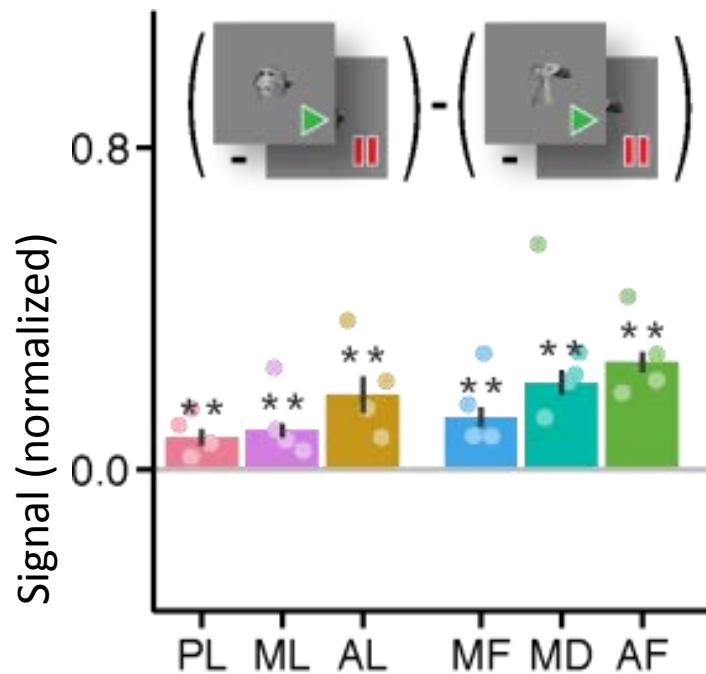
Object Motion-Sensitive



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Source: Fisher, Clark, and Winrich A. Freiwald. "Contrasting specializations for facial motion  
within the macaque face-processing system." *Current Biology* 25, no. 2 (2015): 261-266.

# The macaque face processing system: Sensitivity to stimulus motion

Face Shape-Motion Interaction



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Source: Fisher, Clark, and Winrich A. Freiwald. "Contrasting specializations for facial motion  
within the macaque face-processing system." *Current Biology* 25, no. 2 (2015): 261-266.

Moving



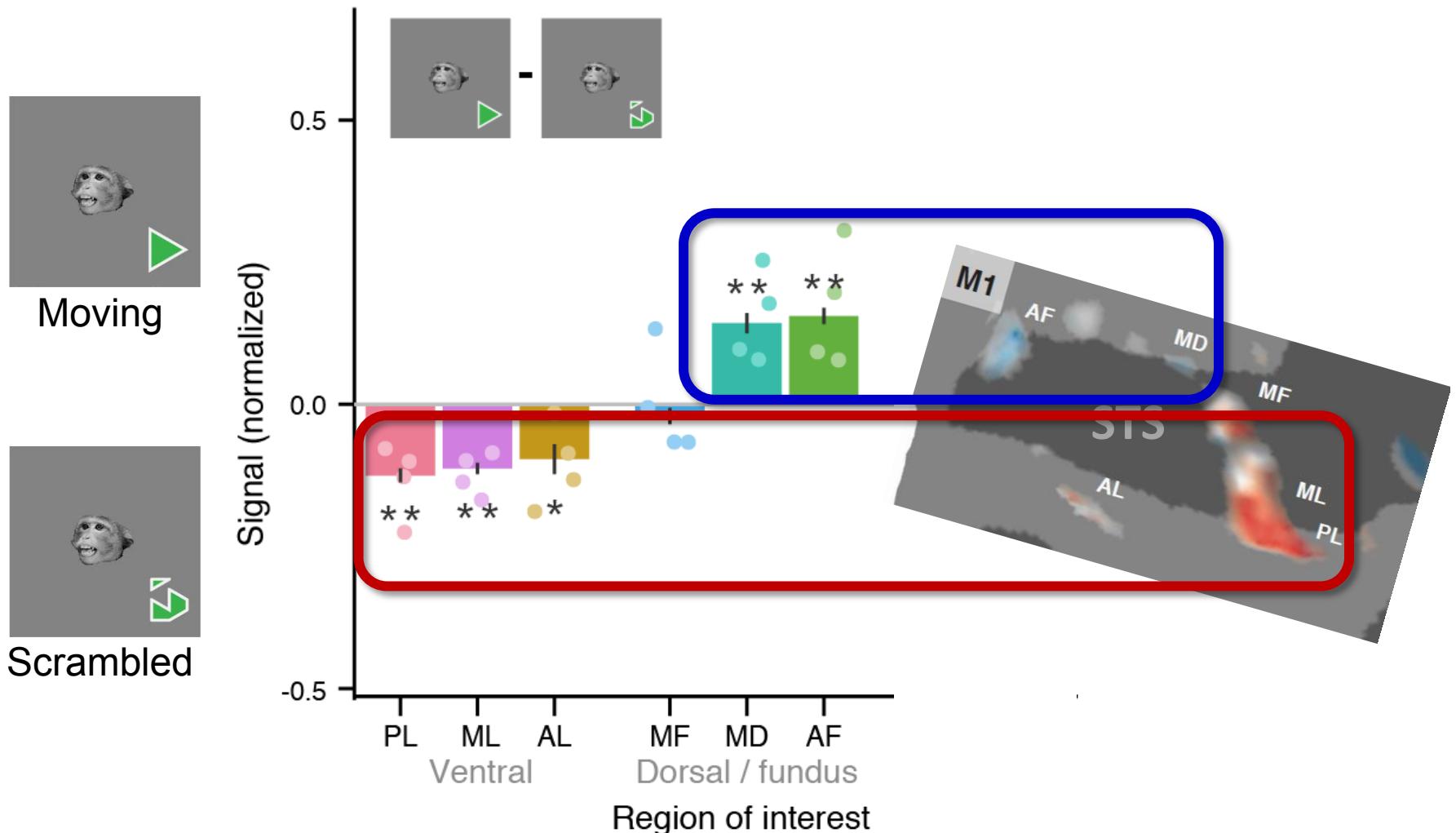
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Still



**Motion?**  
**Image content?**  
**Update frequency?**

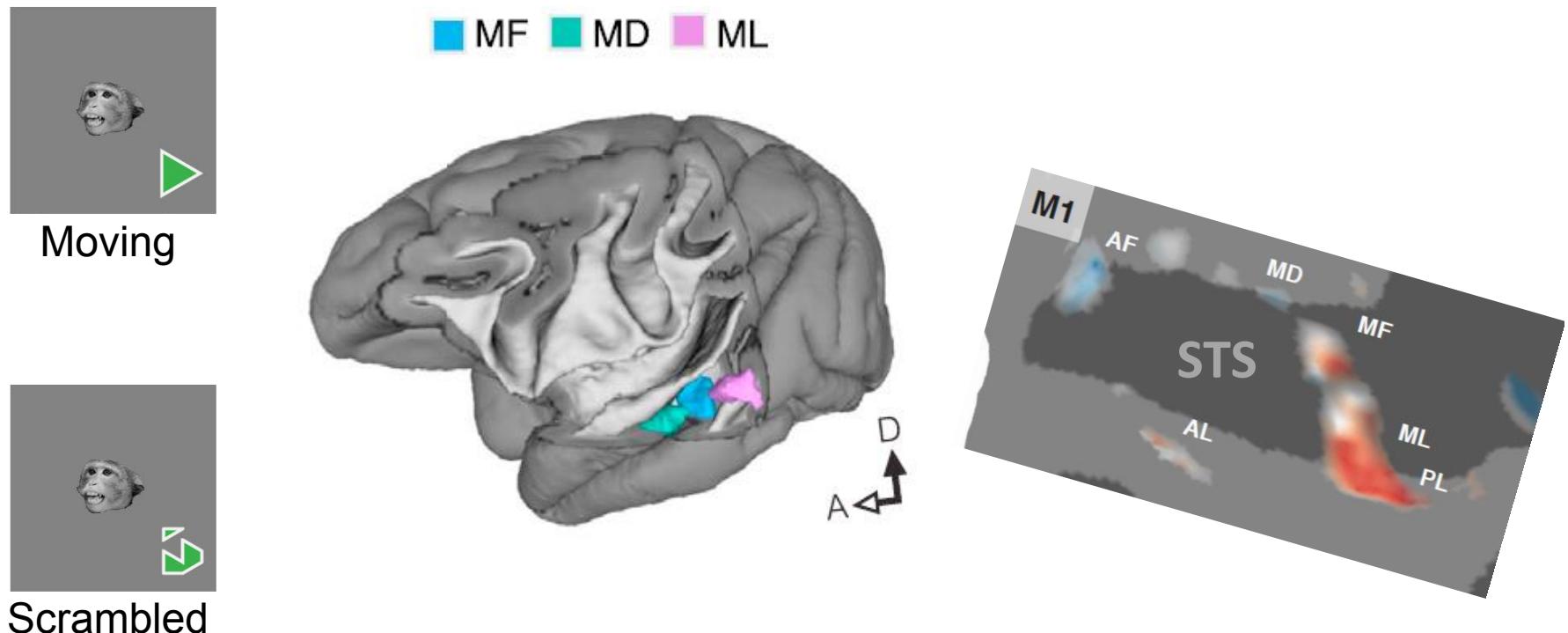
# The macaque face processing system: A new Functional Division



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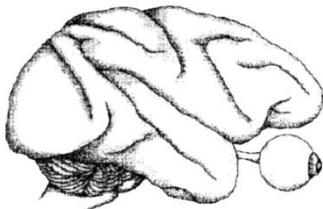
Source: Fisher, Clark, and Winrich A. Freiwald. "Contrasting specializations for facial motion within the macaque face-processing system." Current Biology 25, no. 2 (2015): 261-266.

# The macaque face processing system: A new Functional Division

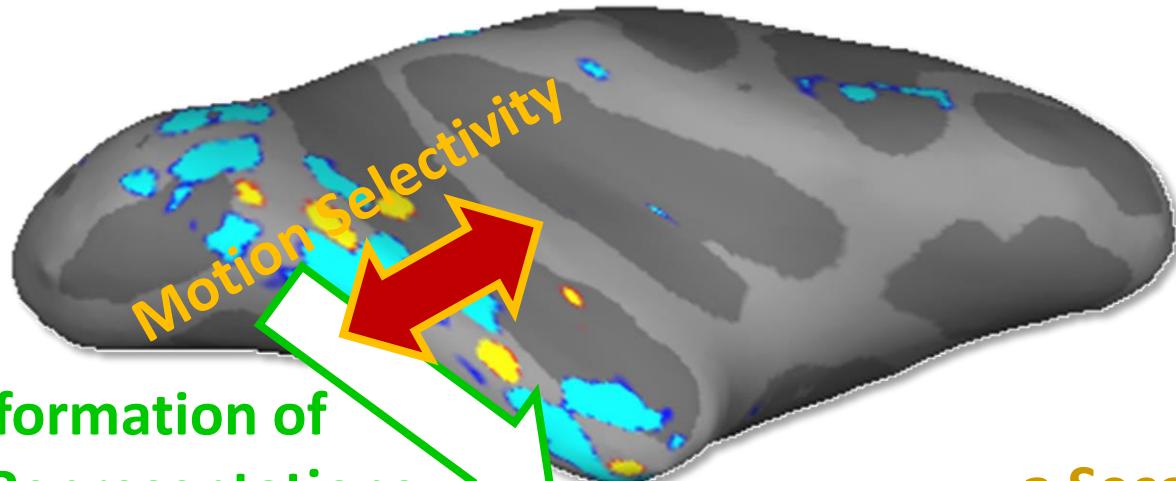


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Source: Fisher, Clark, and Winrich A. Freiwald. "Contrasting specializations for facial motion within the macaque face-processing system." *Current Biology* 25, no. 2 (2015): 261-266.

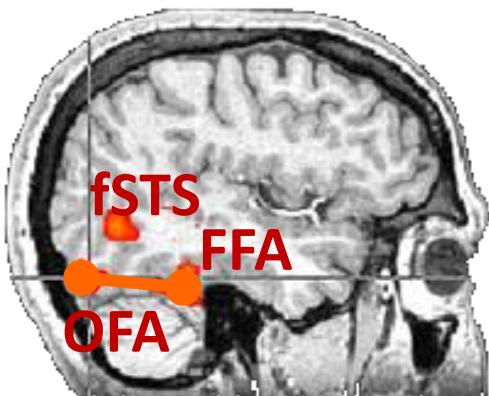


# The macaque face processing system: two axes of functional specialization



**Transformation of  
Face Representations  
from Picture to Identity**

**a Second  
Face-Processing System**

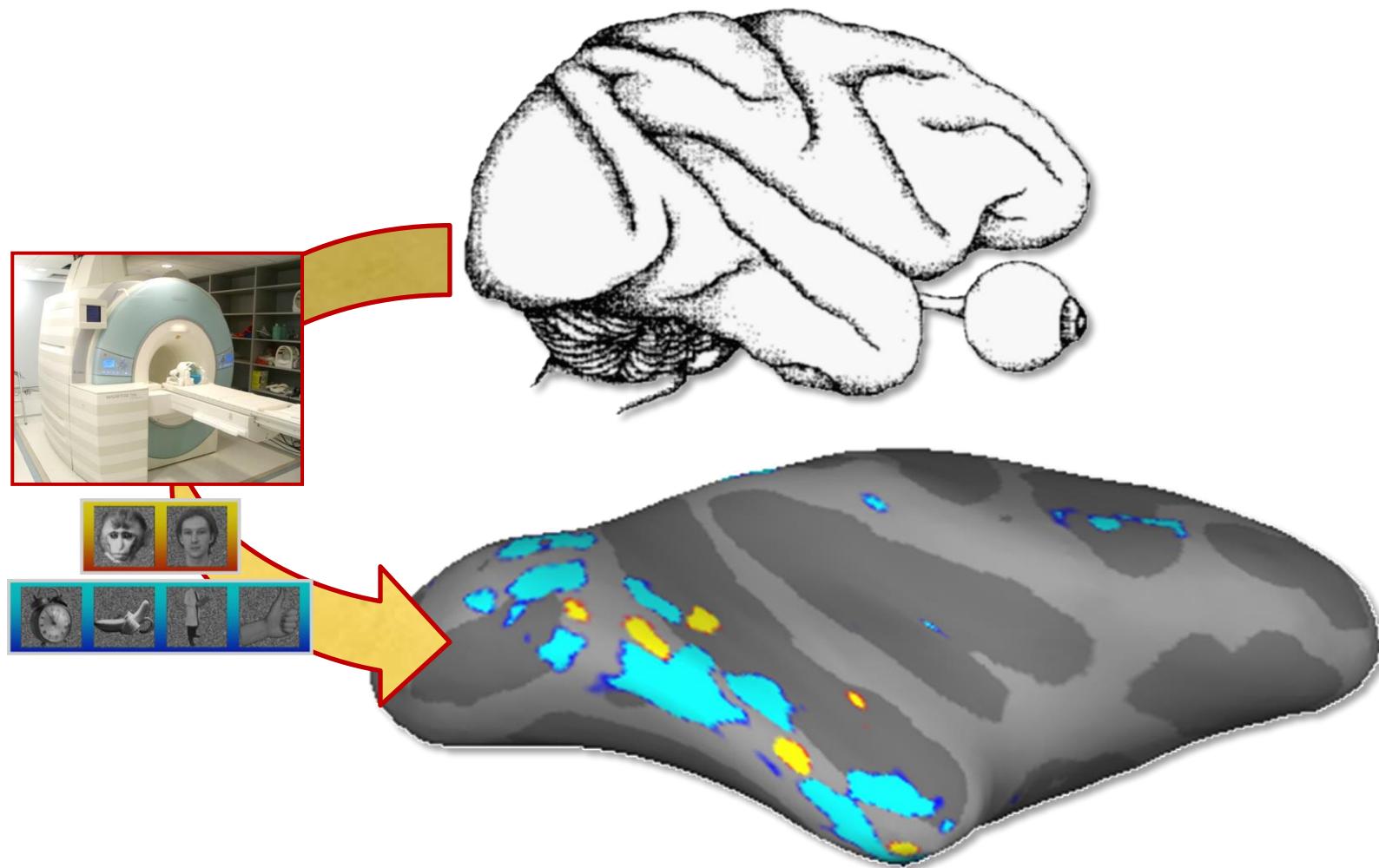


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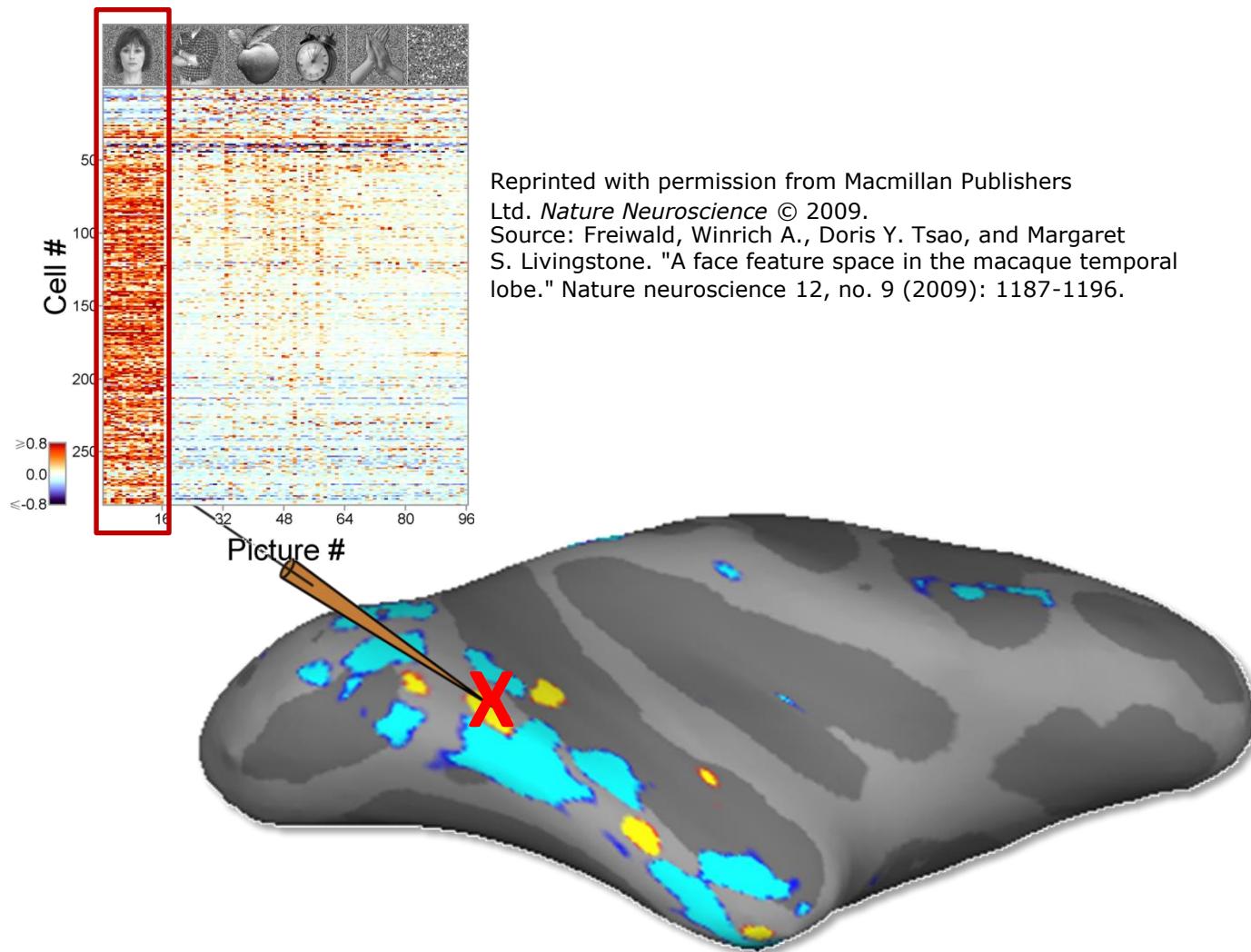
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# The Neural Circuits of Face Processing

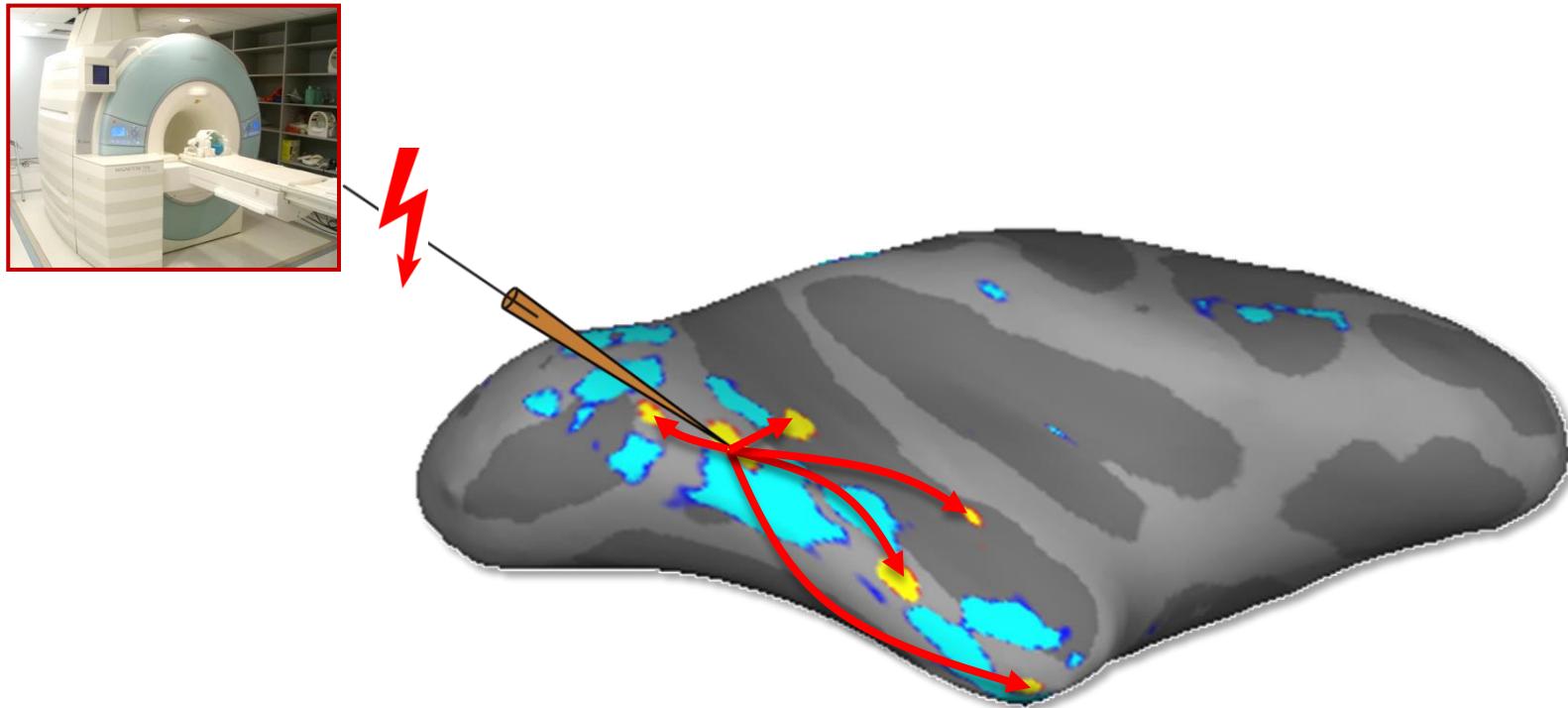


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# The Neural Circuits of Face Processing

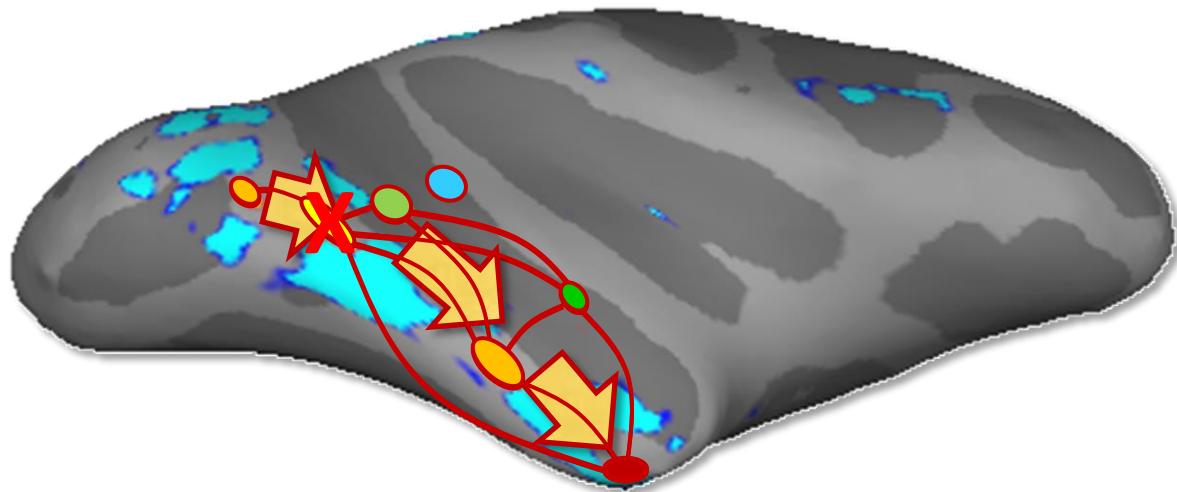


# The Neural Circuits of Face Processing



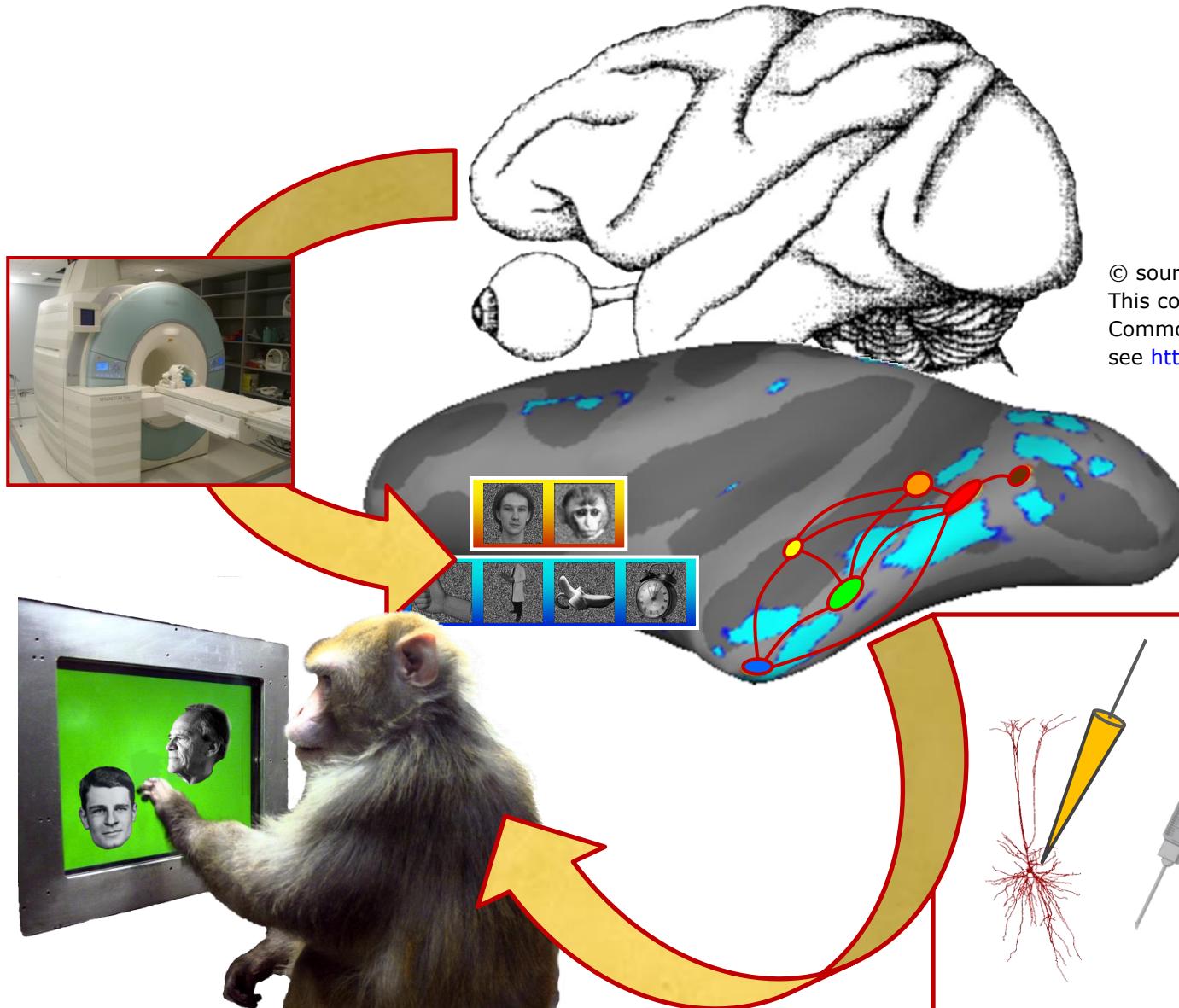
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# The Neural Circuits of Face Processing



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# Neural Circuit Analysis



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