
Of Primates, Faces, and Intelligence

Winrich Freiwald, PhD



SCIENCE FOR THE BENEFIT OF HUMANITY

Octopus

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video.

Octopus

Photos of the life cycle of an octopus
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Wildebeest

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Primates

The Social Intelligence Hypothesis

*Marais, Chance, Jolly ...
Nick Humphrey (1976)
"The social function of intellect"*

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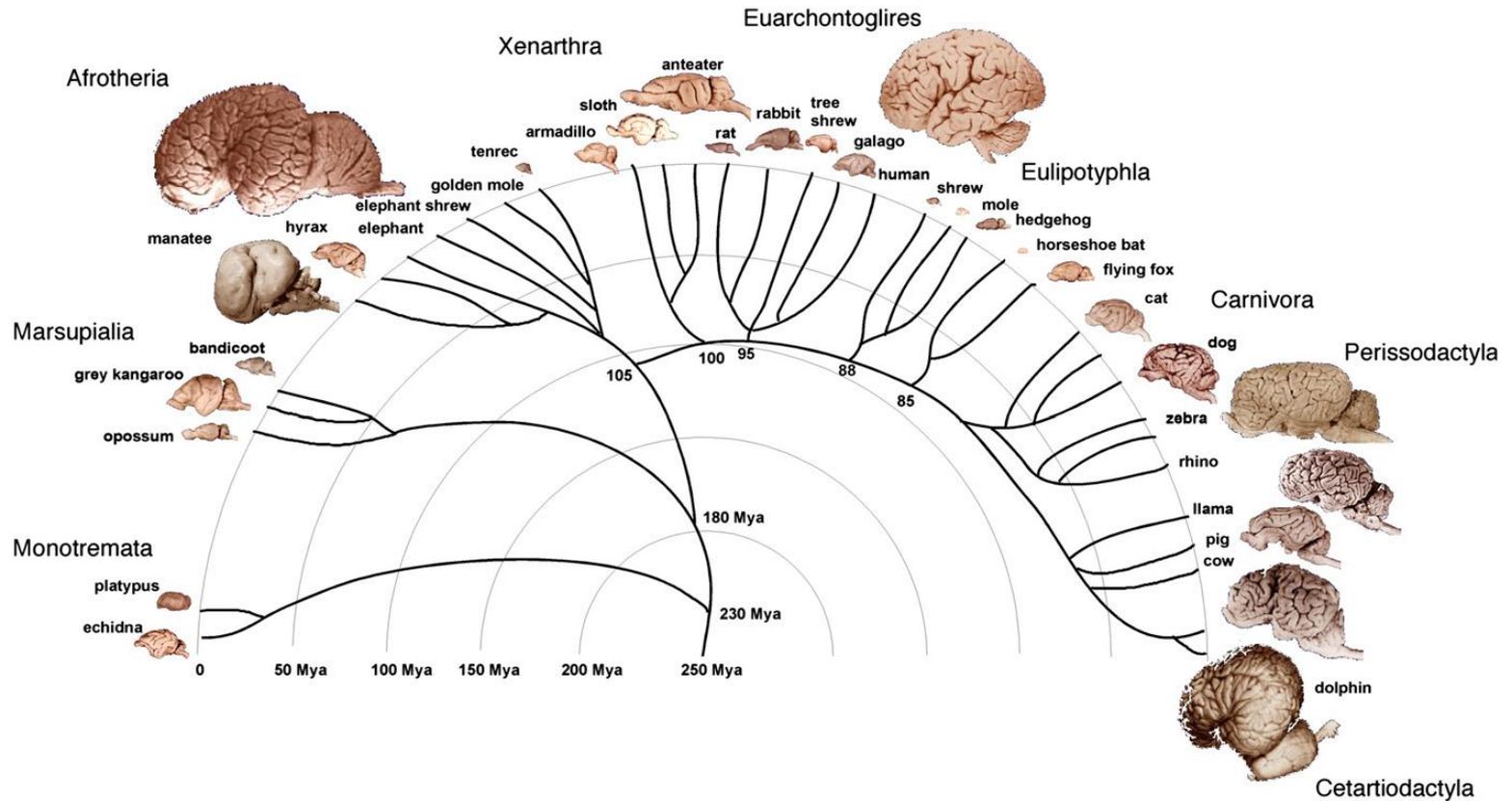
The Primates

- 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 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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Please see lecture video or figure 3 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

Primates



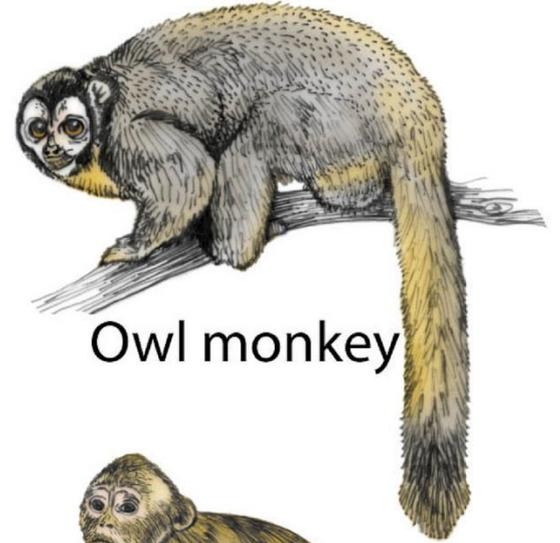
Agouti



18 g 857 M neurons



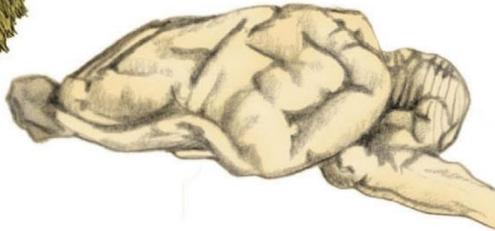
16 g 1468 M neurons



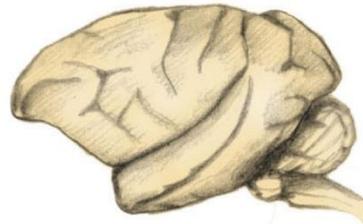
Owl monkey



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

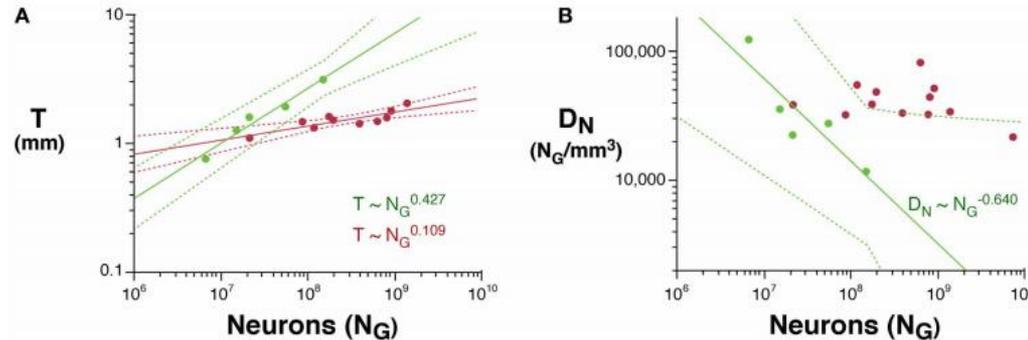


FIGURE 2 | Scaling of average cortical thickness (A) and of average neuronal density (B) as a function of numbers of cortical neurons in rodents (green) and primates (red). Power functions, where the exponents

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 gyrification 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

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

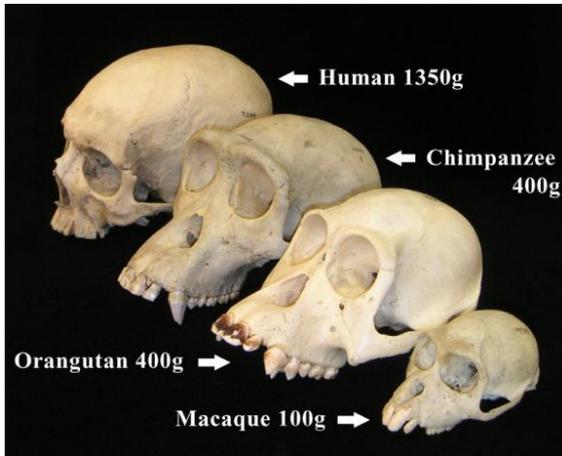


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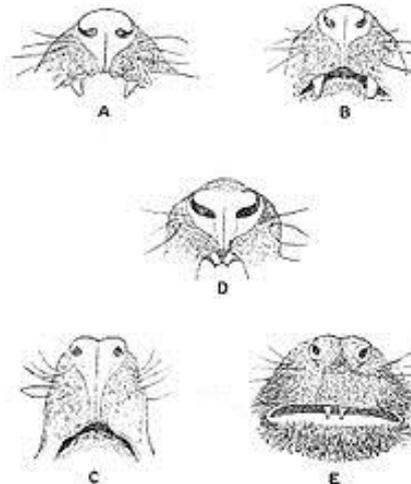
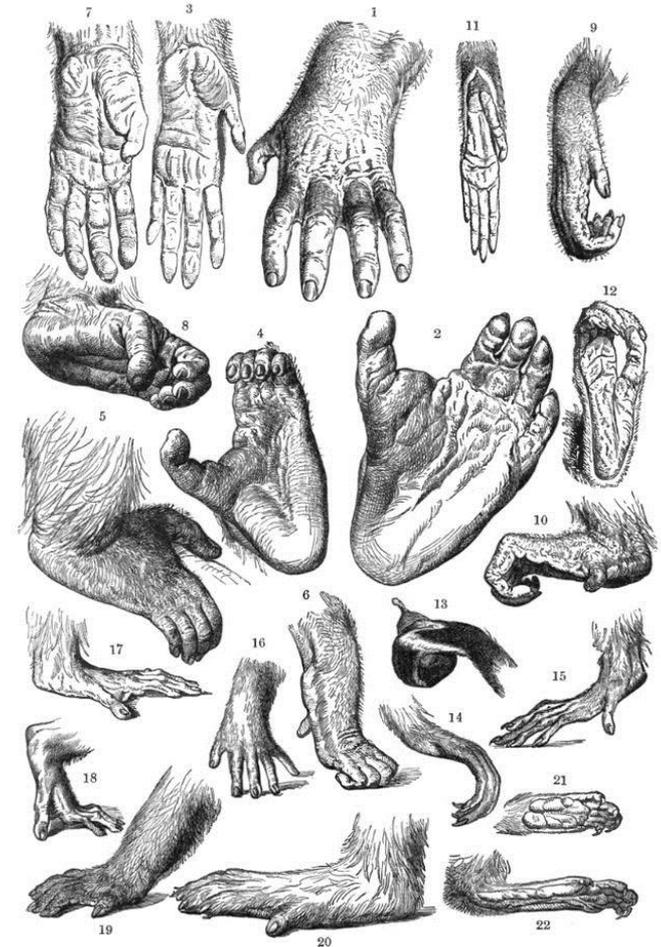


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HANDS AND FEET OF APES AND MONKEYS.
1, 2, Gorilla; 3-8, Chimpanzee; 9, 10, Orang; 11, 13, Gibbon; 14, 15, Guereza; 16-18, Macaque; 19, 20, Baboon; 21, 22, Marmoset.

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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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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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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 truncatus*), 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.

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u.tv/video/cerimes/l_univers_social_des_ma
caques.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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Structure of Primate Social Knowledge

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from Neurons to Minds

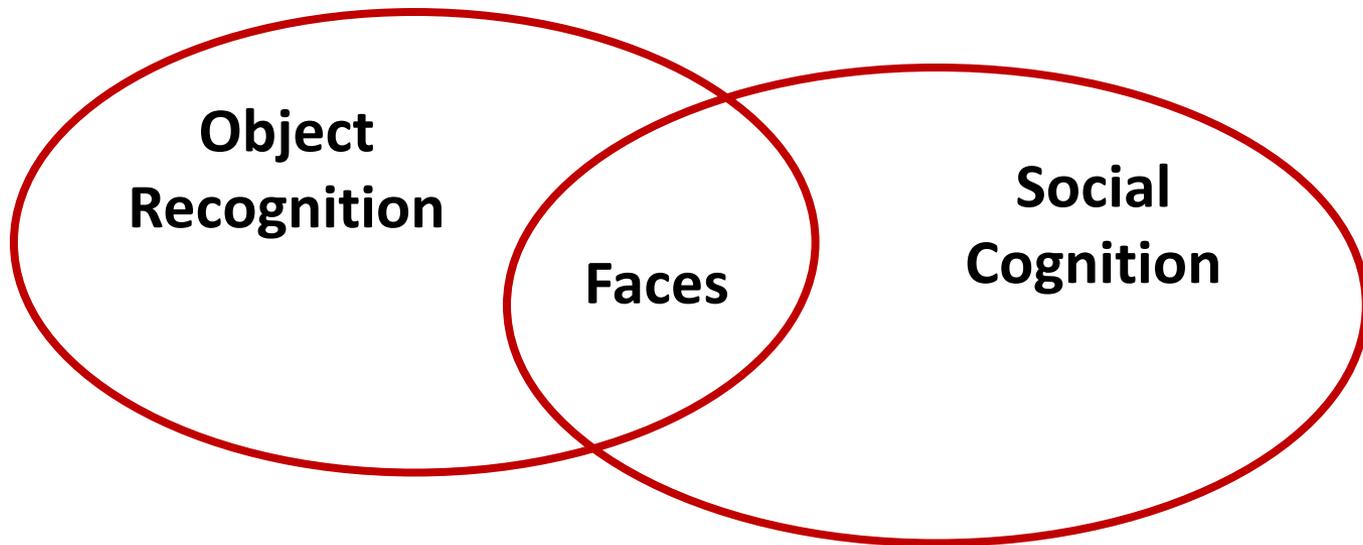


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Daniel J., and David C. Van Essen. "Distributed
hierarchical processing in the primate cerebral
cortex." *Cerebral cortex* 1, no. 1 (1991): 1-47.

Gestalt Rules of Perception

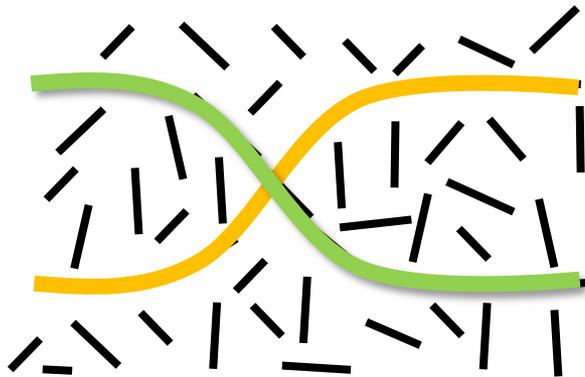
Proximity



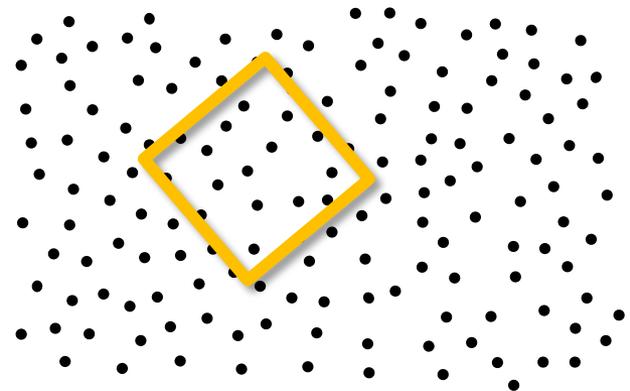
Similarity



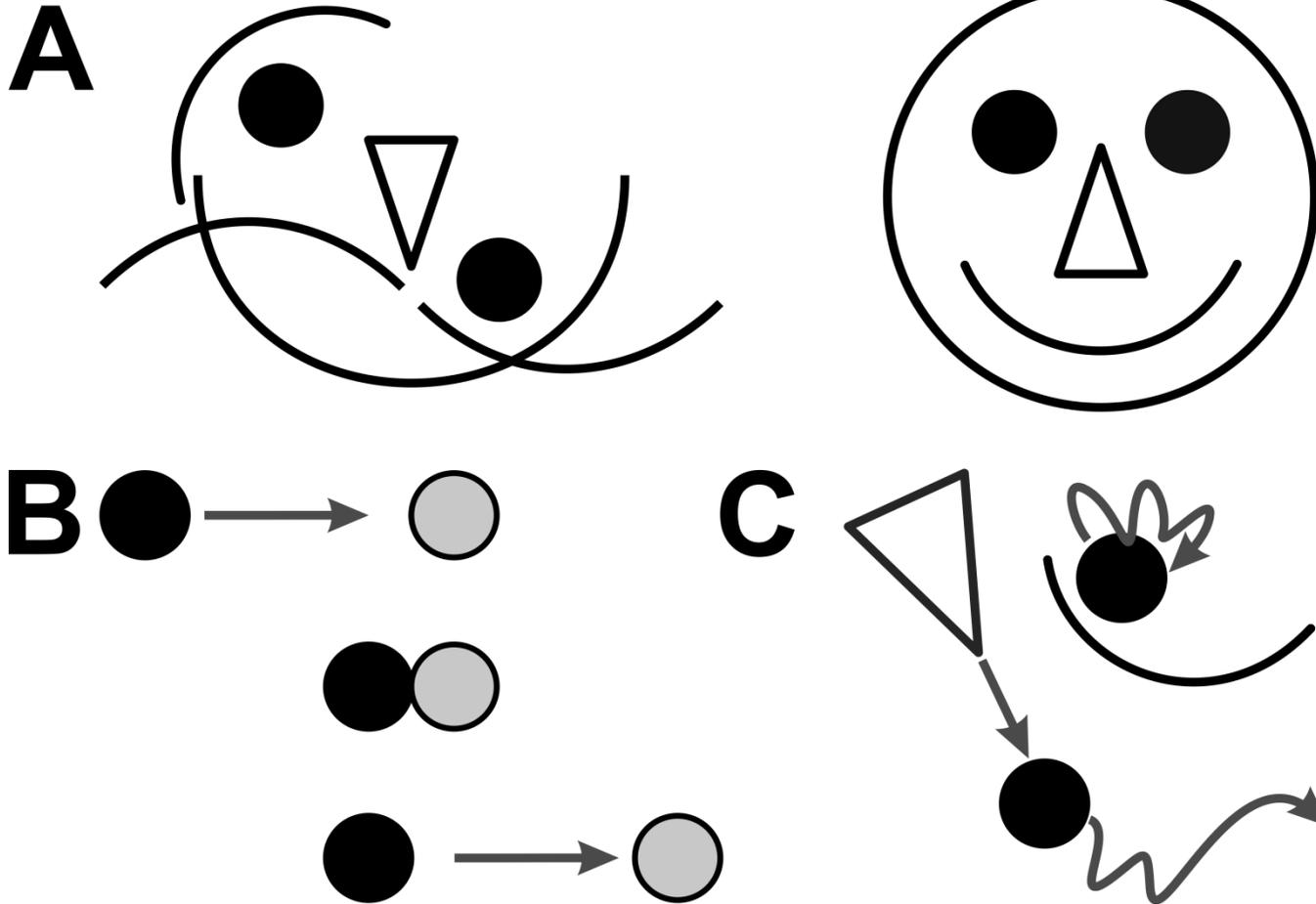
Good Continuation



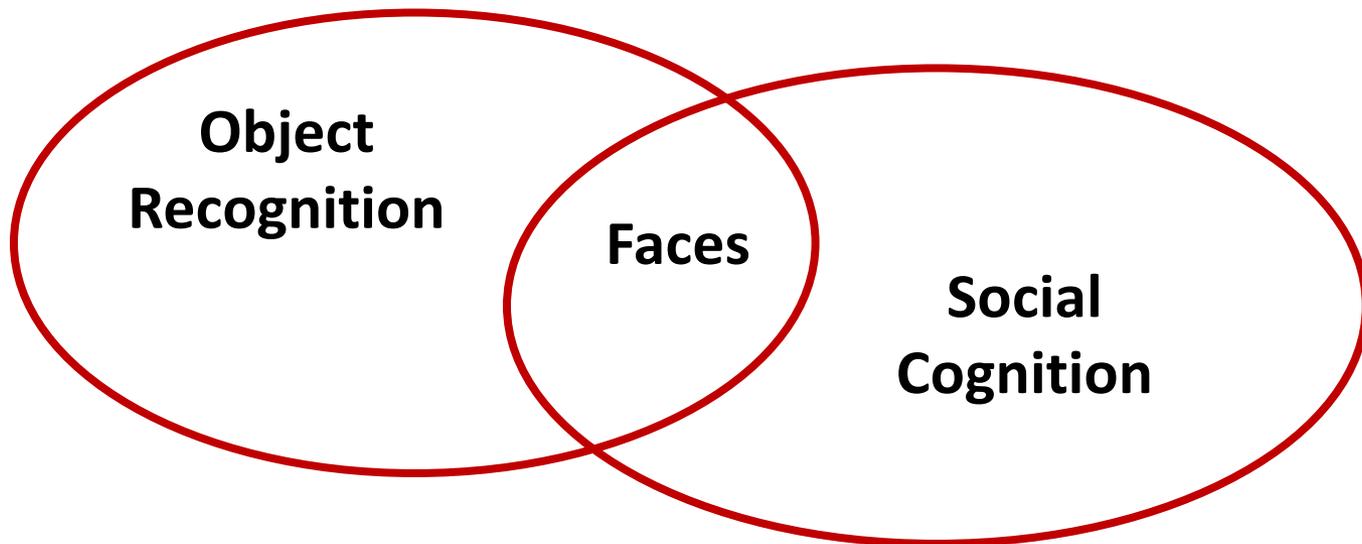
Common Fate



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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The Expression of the Emotions in Man and Animals

Charles Darwin, 1872



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Facial Communication (and lack thereof)

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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)

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Faces elicit automatic emotional, communicative, and cognitive responses

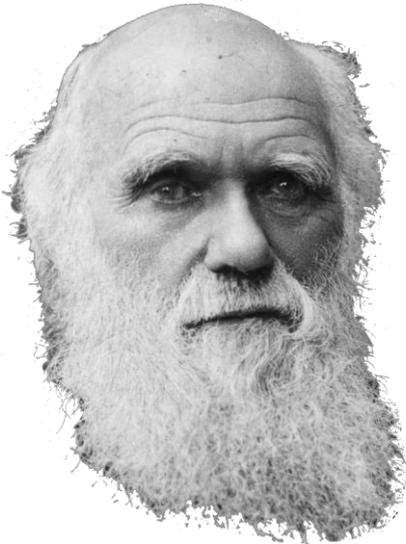


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Faces elicit automatic emotional, communicative, and cognitive responses

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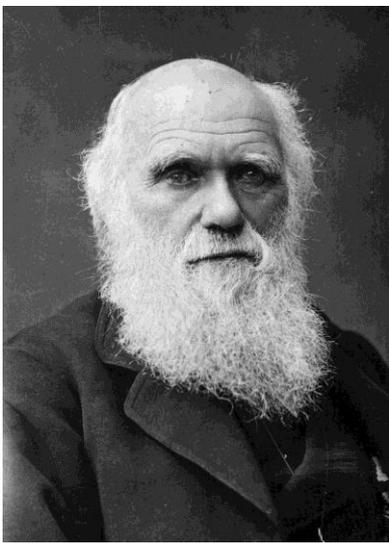


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Social Perception starts with Faces

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

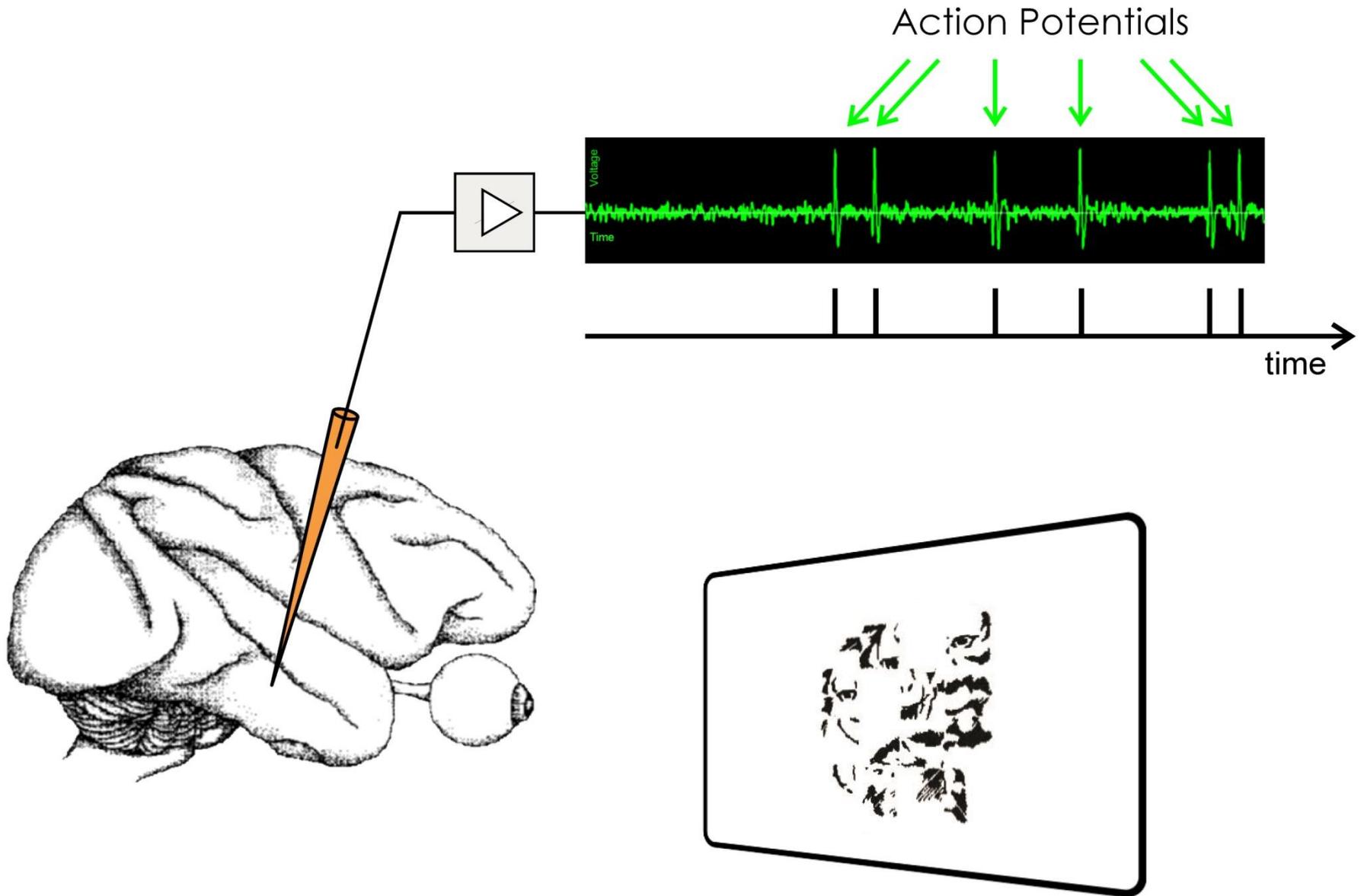


Section of St. Cecilia, Raphael

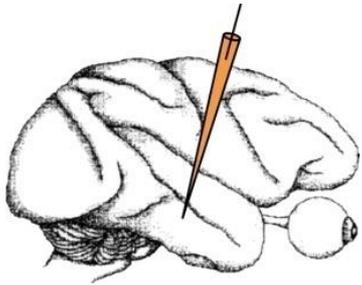
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The Neural Basis of Face Recognition



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Neuropsychologia 46, no. 3 (2008): 841-852.



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The Neural Basis of Face Recognition

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"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

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The Functional Anatomy of Face Recognition

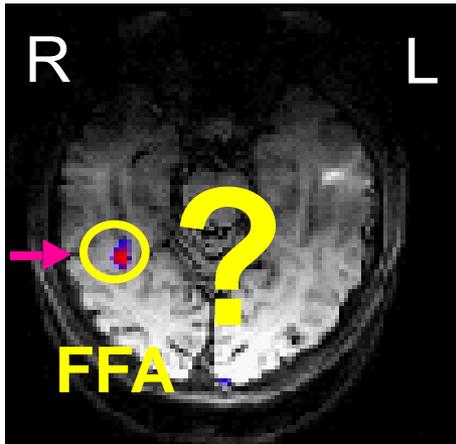
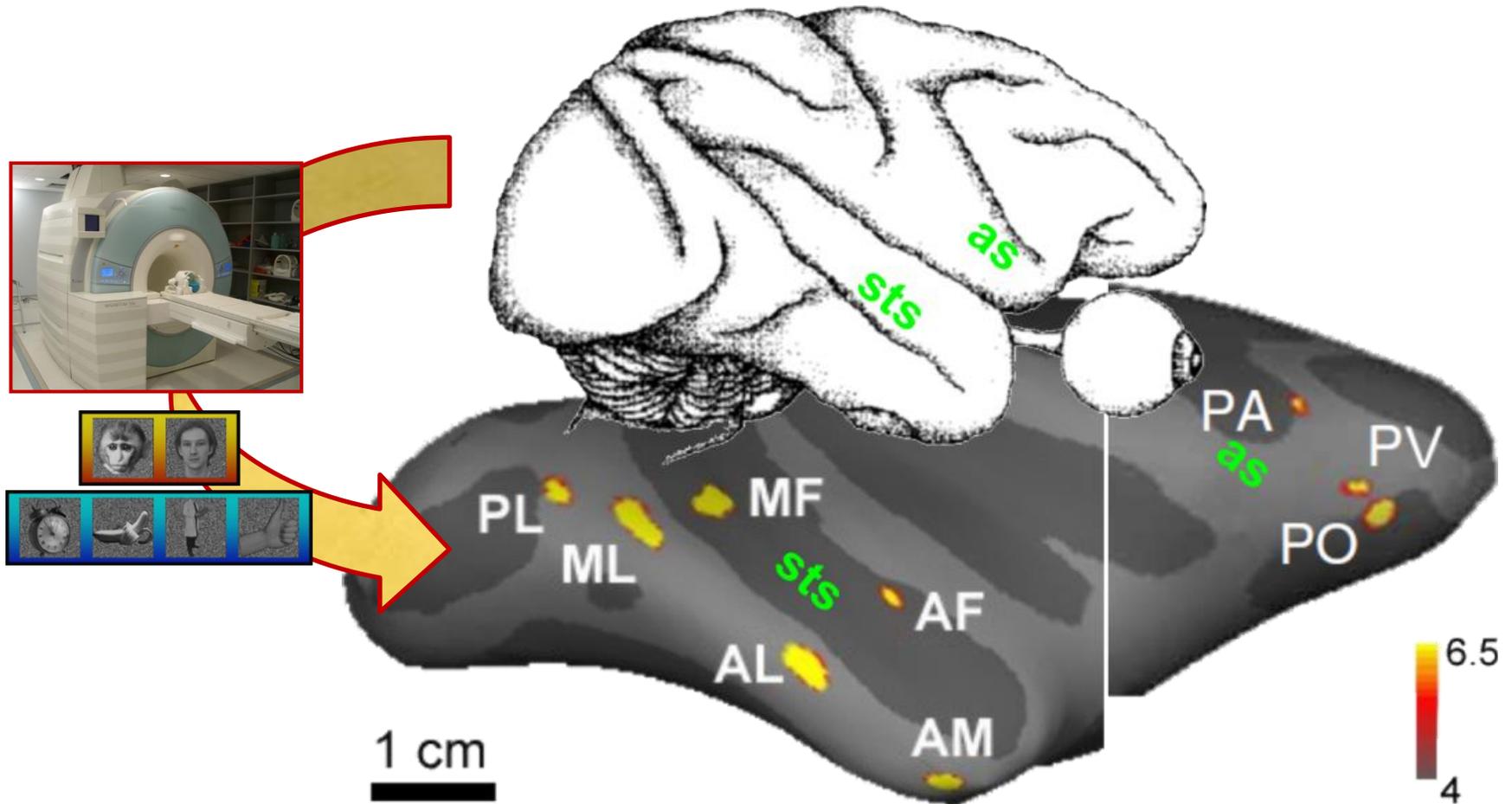


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- Are face areas domain specific modules – or just the tip of the iceberg of face-responsive temporal lobe regions?
- Do monkeys have localized face areas like humans - or not, since electrophysiology seems to suggest broad distribution of face cells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

The macaque face processing system: composition



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The Functional Anatomy of Face Recognition

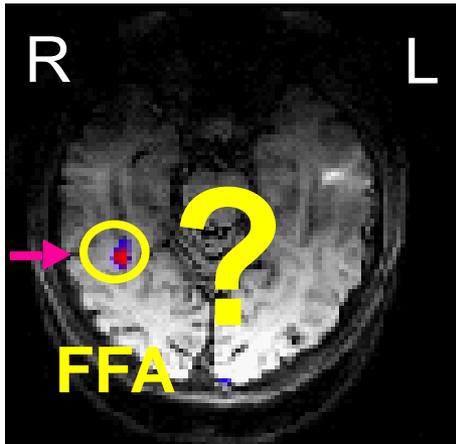
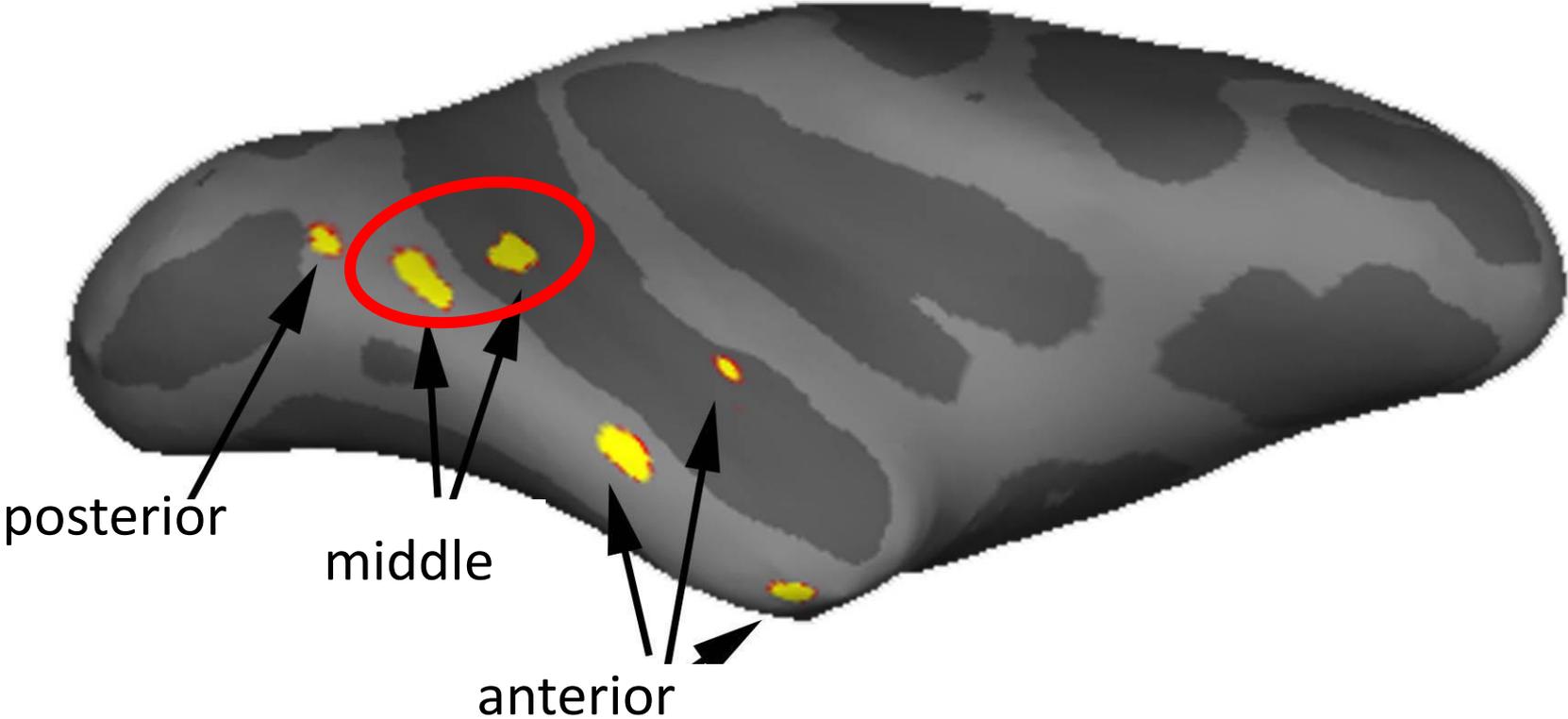
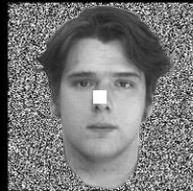


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- Are face areas domain specific modules – or just the tip of the iceberg of face-responsive temporal lobe regions?
- **Monkeys have localized face areas like humans** - or not, since electrophysiology seems to suggest broad distribution of face cells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

How face-selective are the face patches?

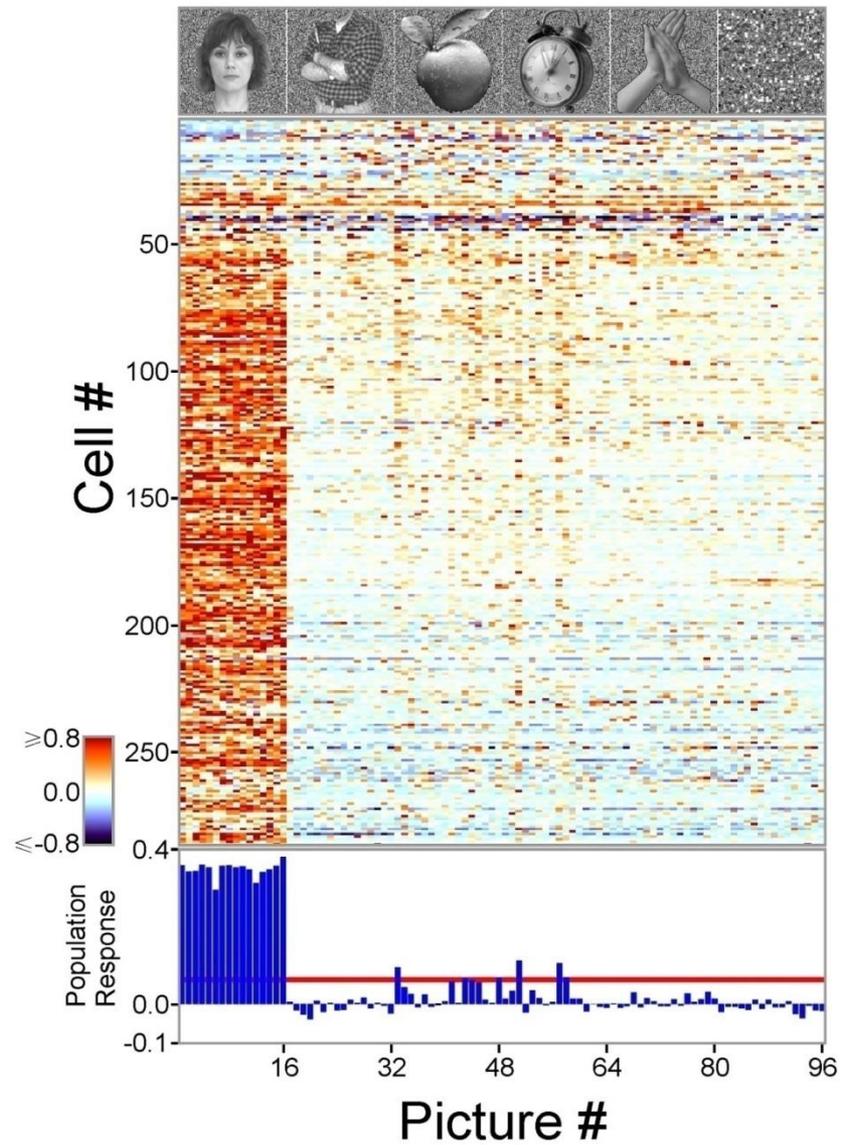




7°

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





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Middle Face Patch Cells

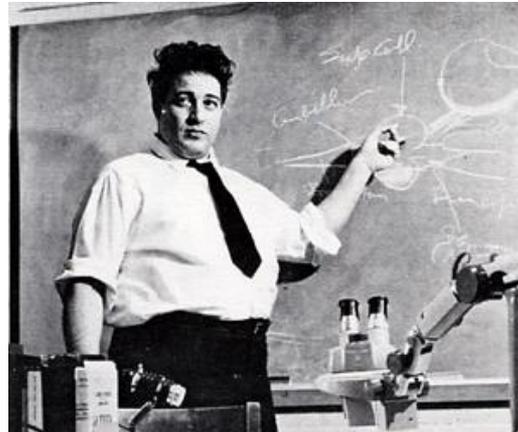
- virtually all are **face selective**
- respond (more weakly) to **non-face objects** that share visual features with faces



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Face cells, hierarchies, grandmother and gnostic neurons

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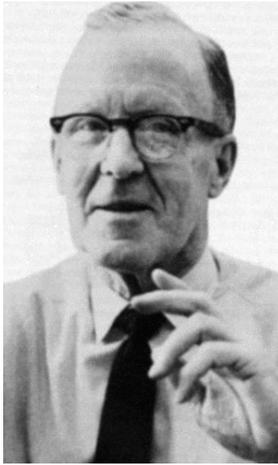


Jerome Lettvin

***David Hubel &
Torsten Wiesel***

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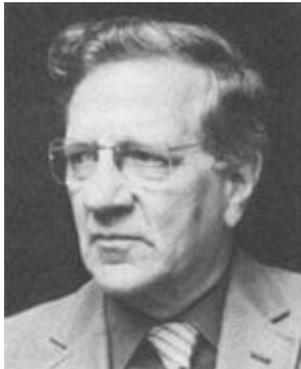
What is the neural code?



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

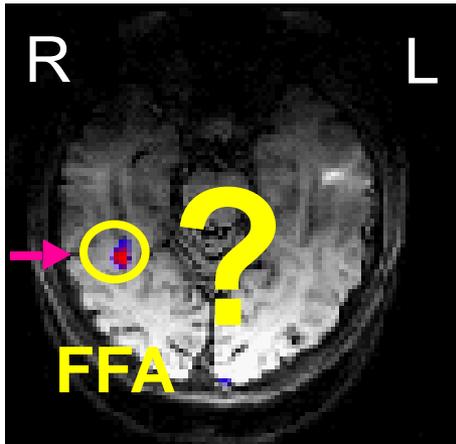


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- **Face patches appear to be dedicated domain specific modules** – or just the tip of the iceberg of face responsive temporal lobe regions? ✓
- **Monkeys have localized face areas like humans** - or not, since electrophysiology seems to suggest broad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

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

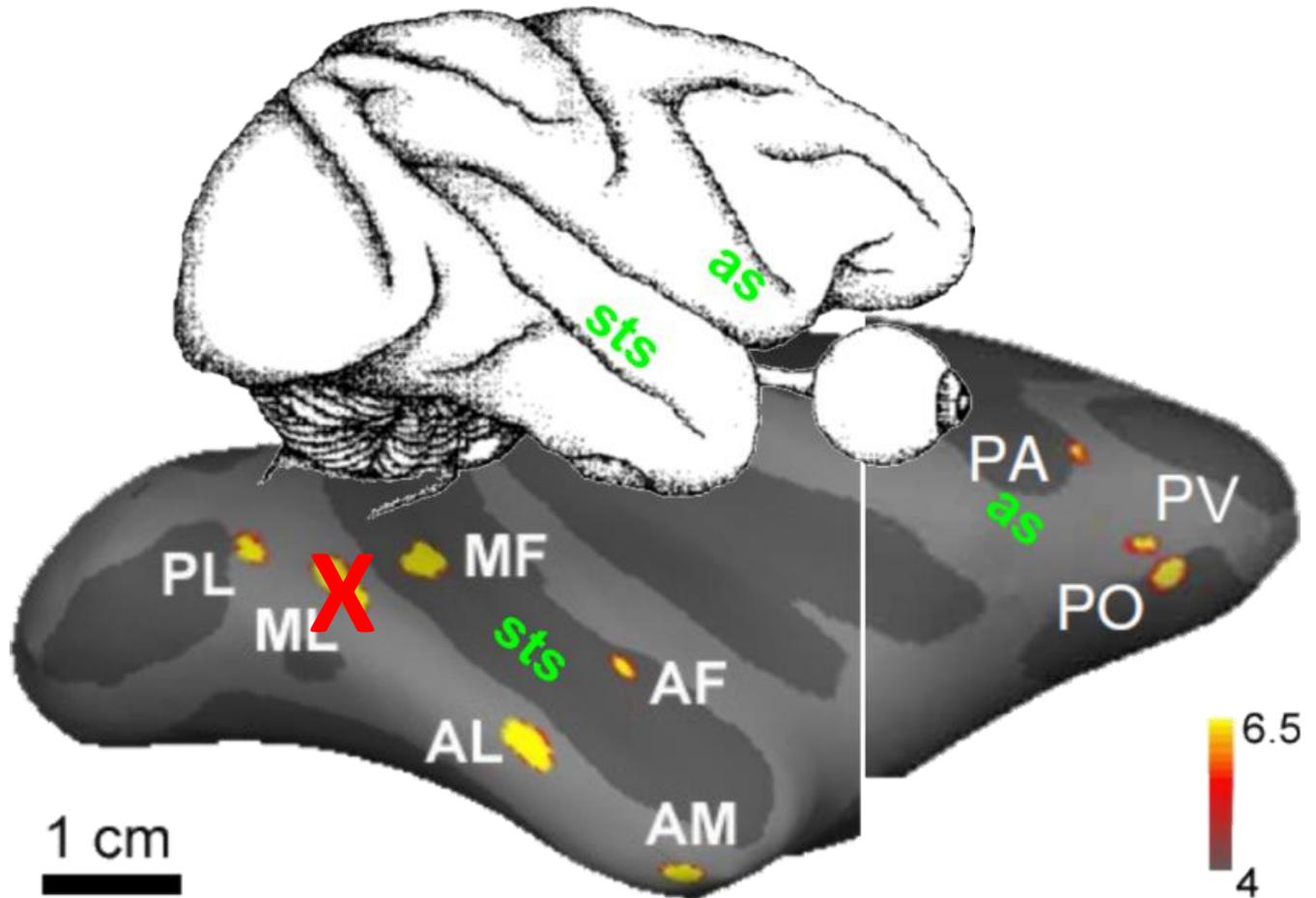
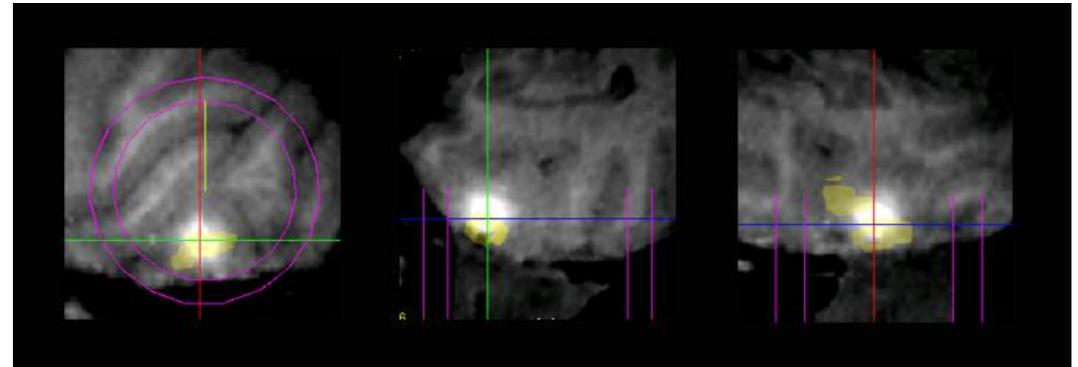
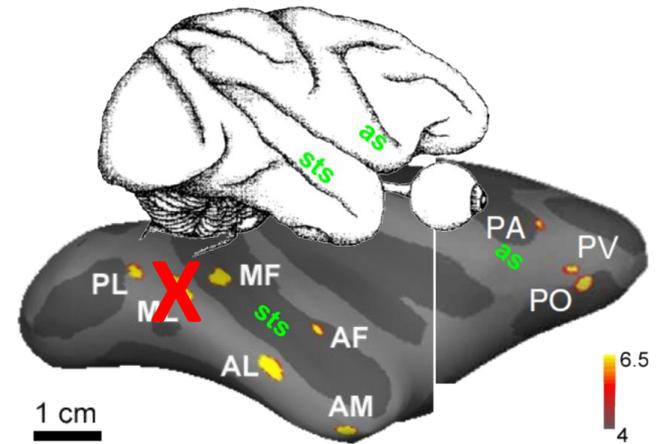
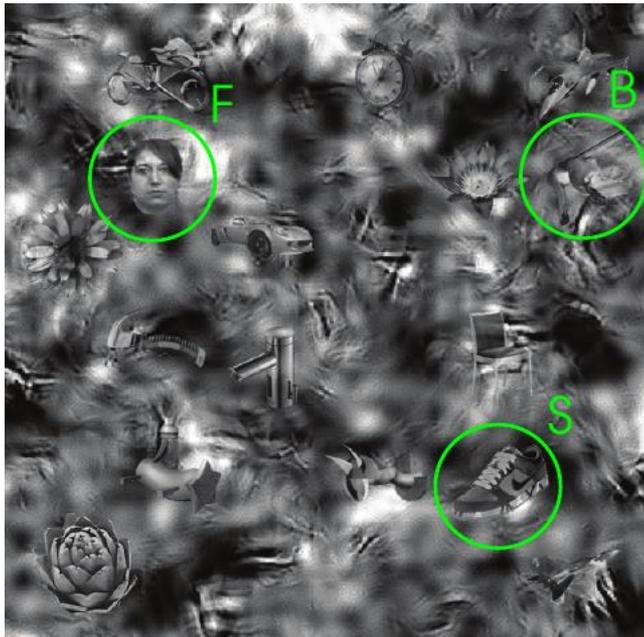
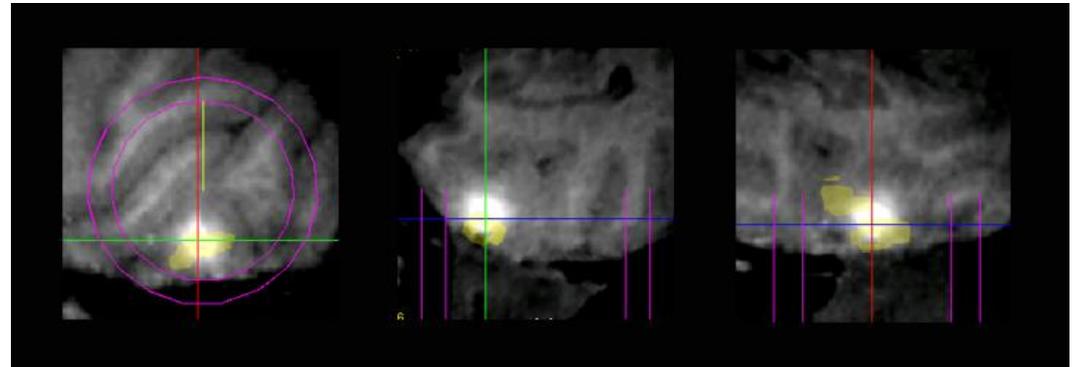
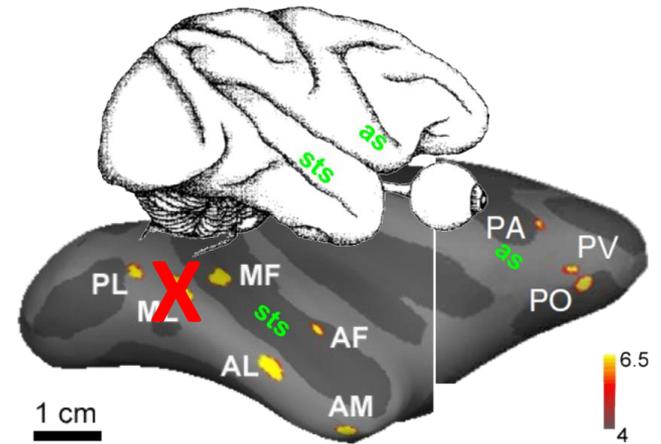
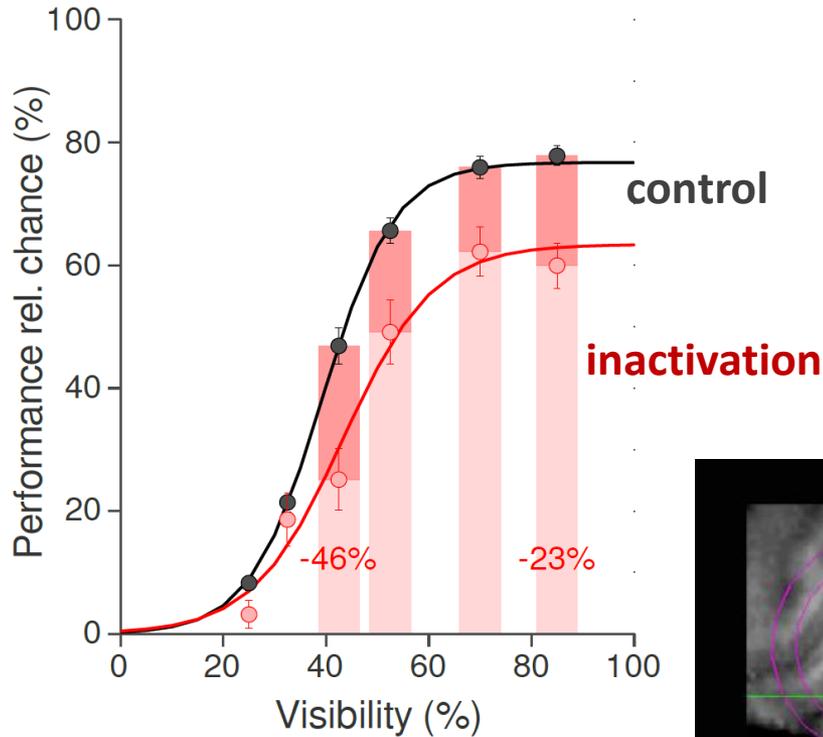


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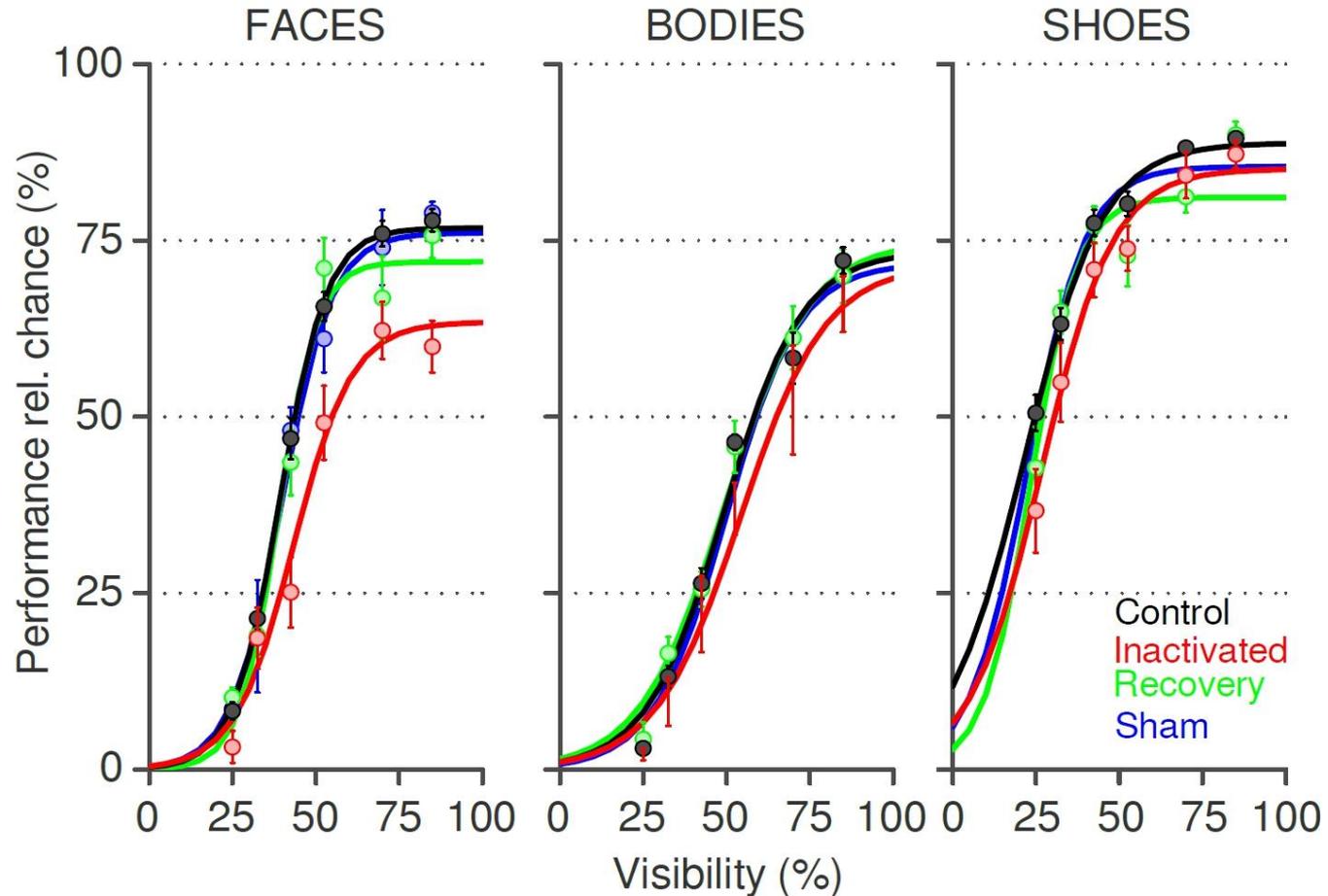
The macaque face processing system: causal role in face detection

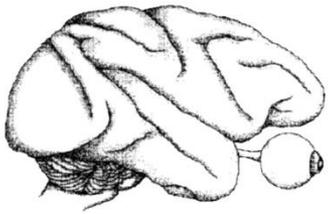


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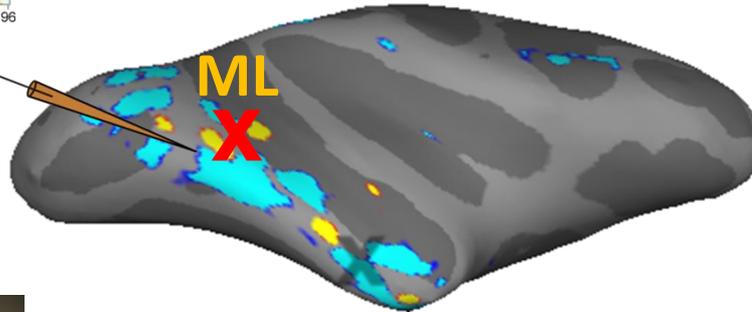
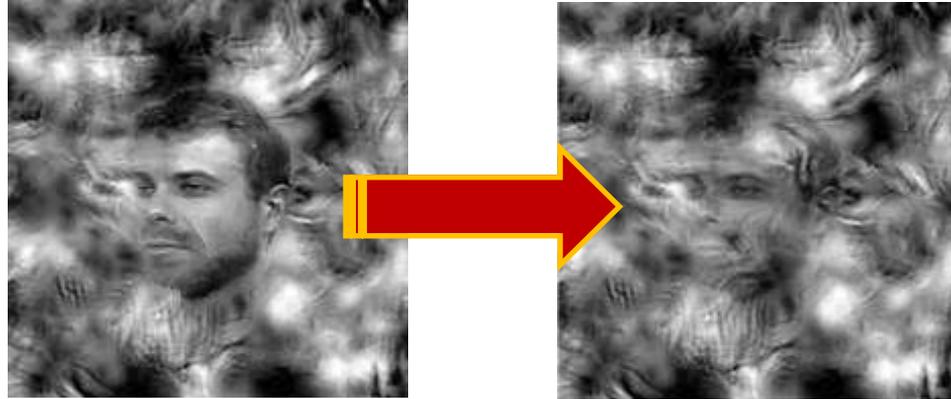
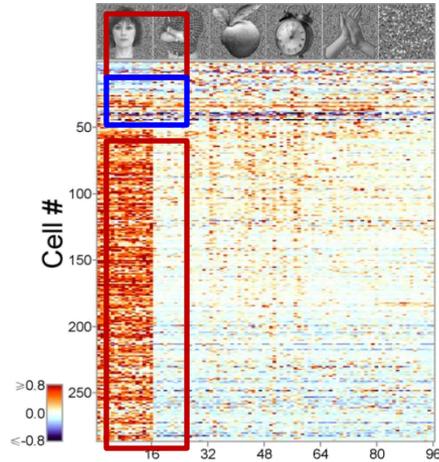


The macaque face processing system: causal role in face detection



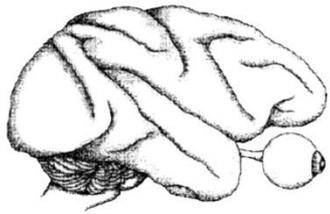


The macaque face processing system: face-domain specific modularity

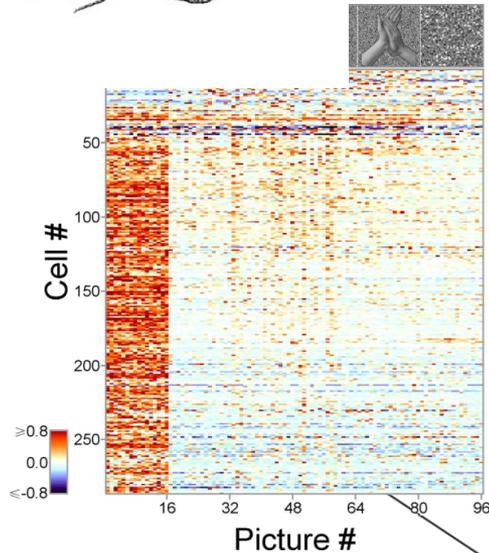


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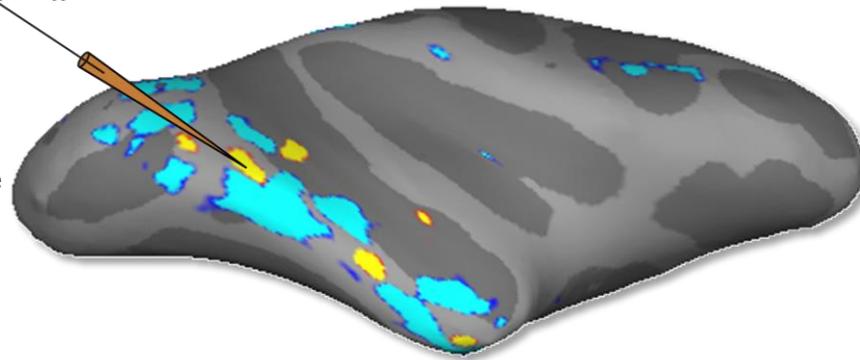




The macaque face processing system

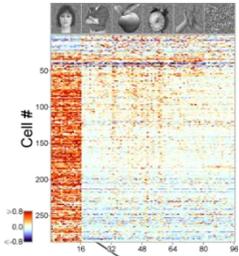


We have **unprecedented access** to functionally **homogenous populations** of cells coding for **one high-level object category**

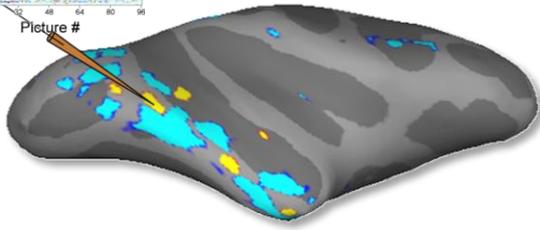


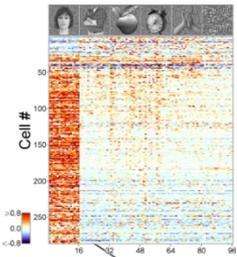
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Source: Freiwald, Winrich A., Doris Y. Tsao, and Margaret S. Livingstone "A face feature space in the macaque temporal lobe." *Nature neuroscience* 12, no. 9 (2009): 1187-1196.

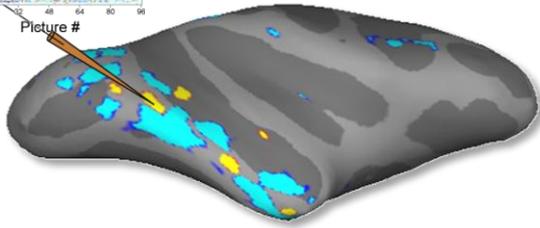


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Source: Freiwald, Winrich A., Doris Y. Tsao, and Margaret S. Livingstone. "A face feature space in the macaque temporal lobe." *Nature neuroscience* 12, no. 9 (2009): 1187-1196.



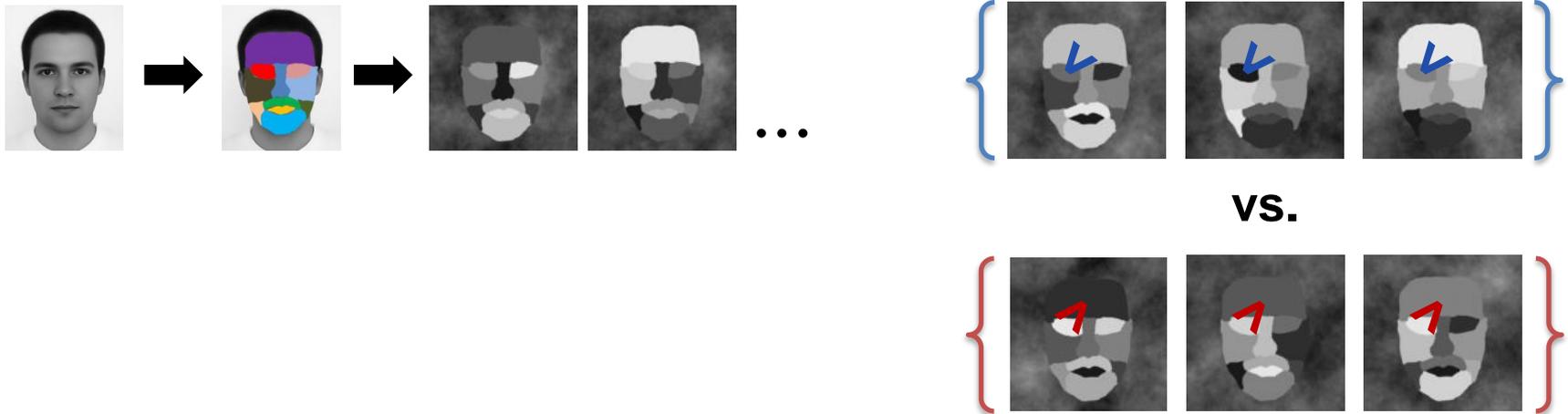


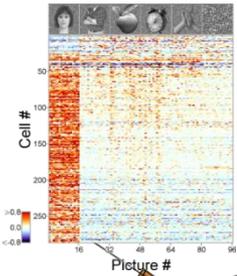
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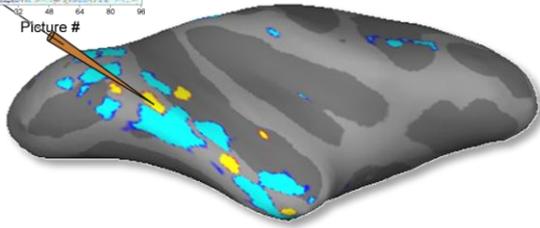
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Human Psychophysics



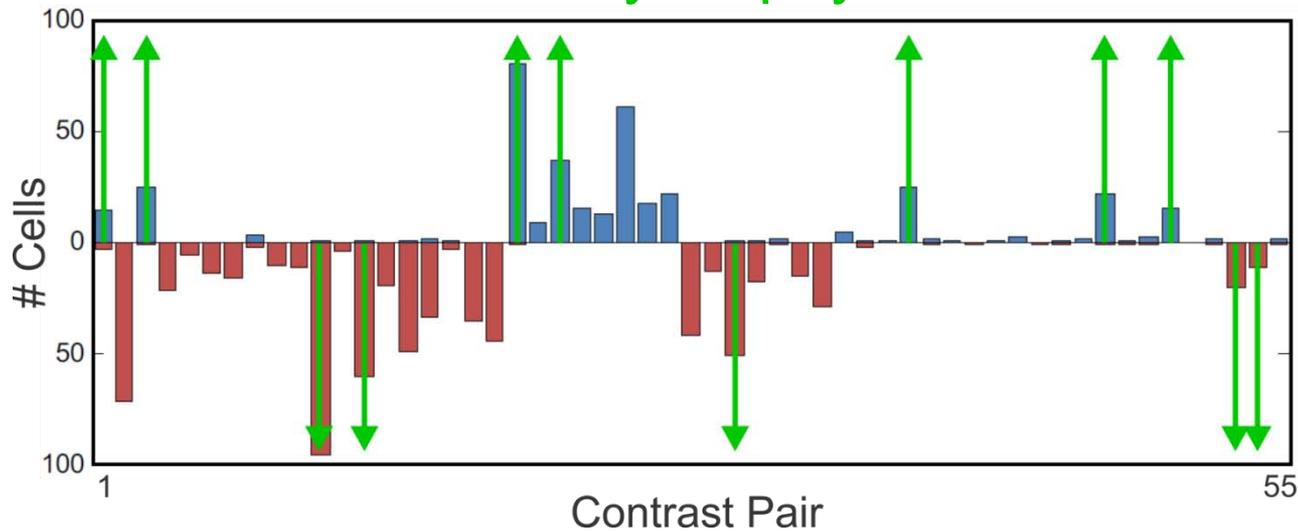


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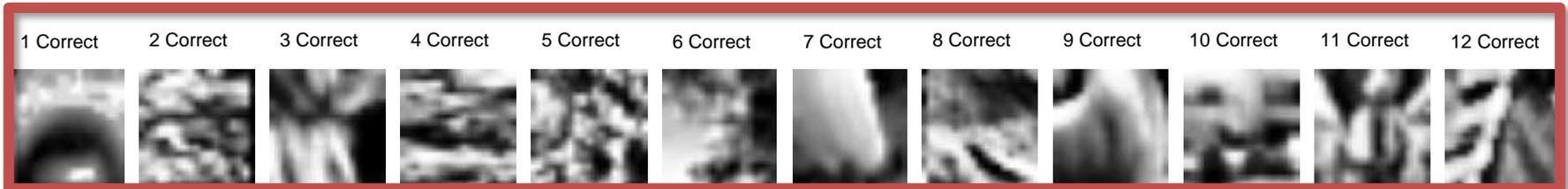
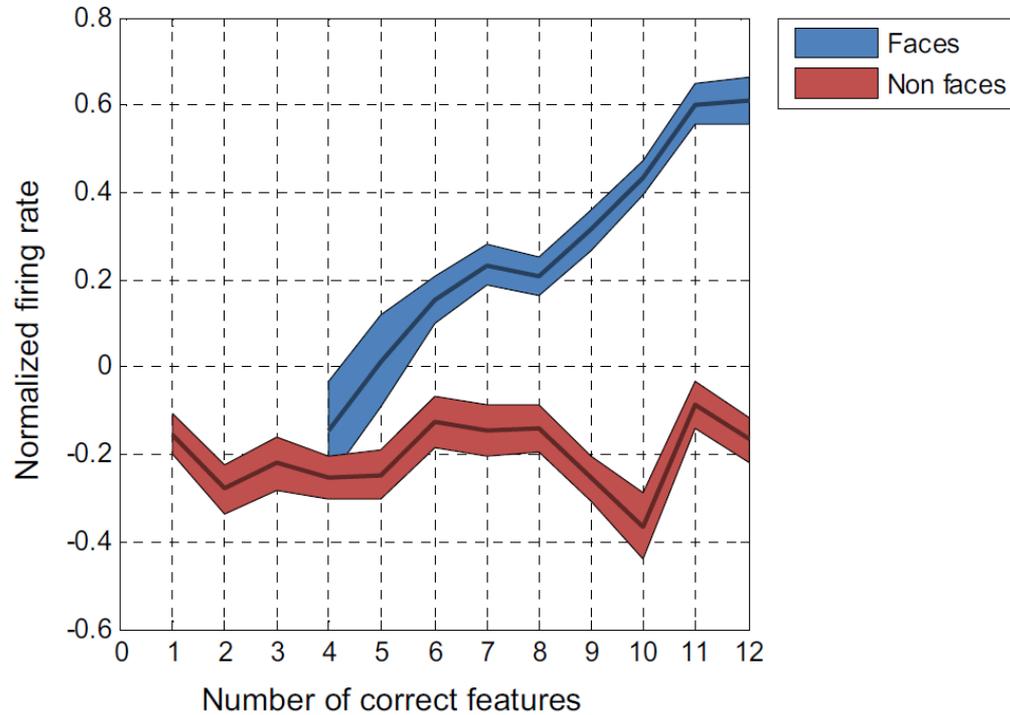
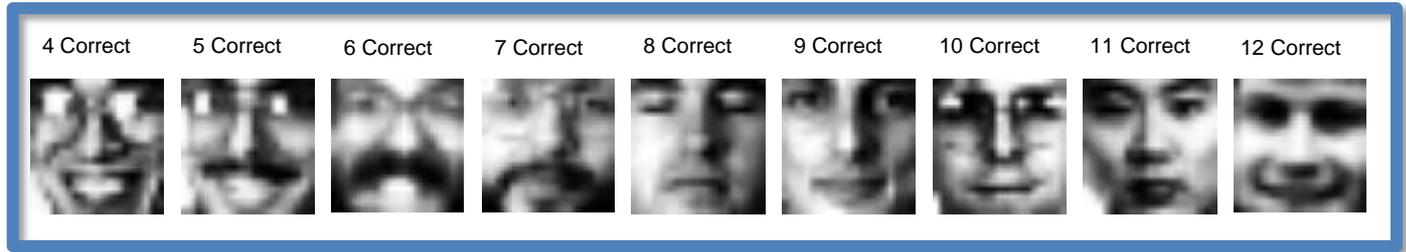


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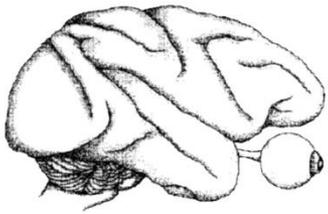
Human Psychophysics



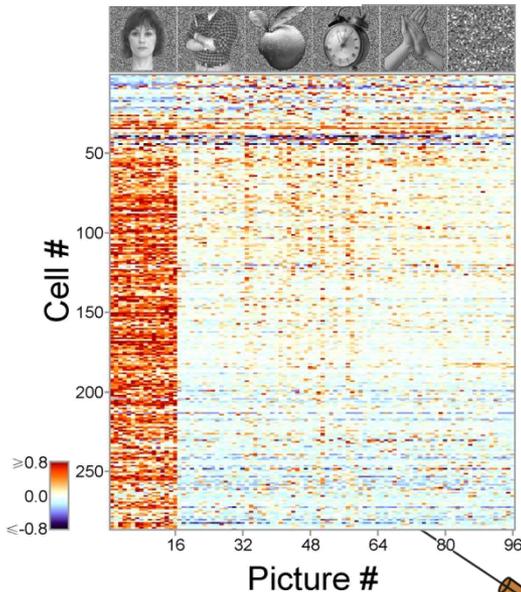
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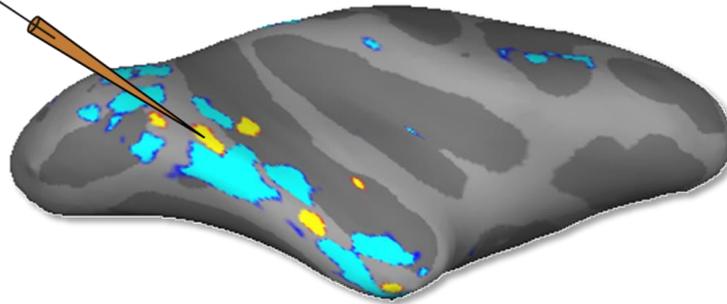
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 Source: Ohayon, Shay, Winrich A. Freiwald, and Doris Y. Tsao. "What makes a cell face selective? The importance of contrast." *Neuron* 74, no. 3 (2012): 567-581.



The macaque face processing system: The Part and the Whole



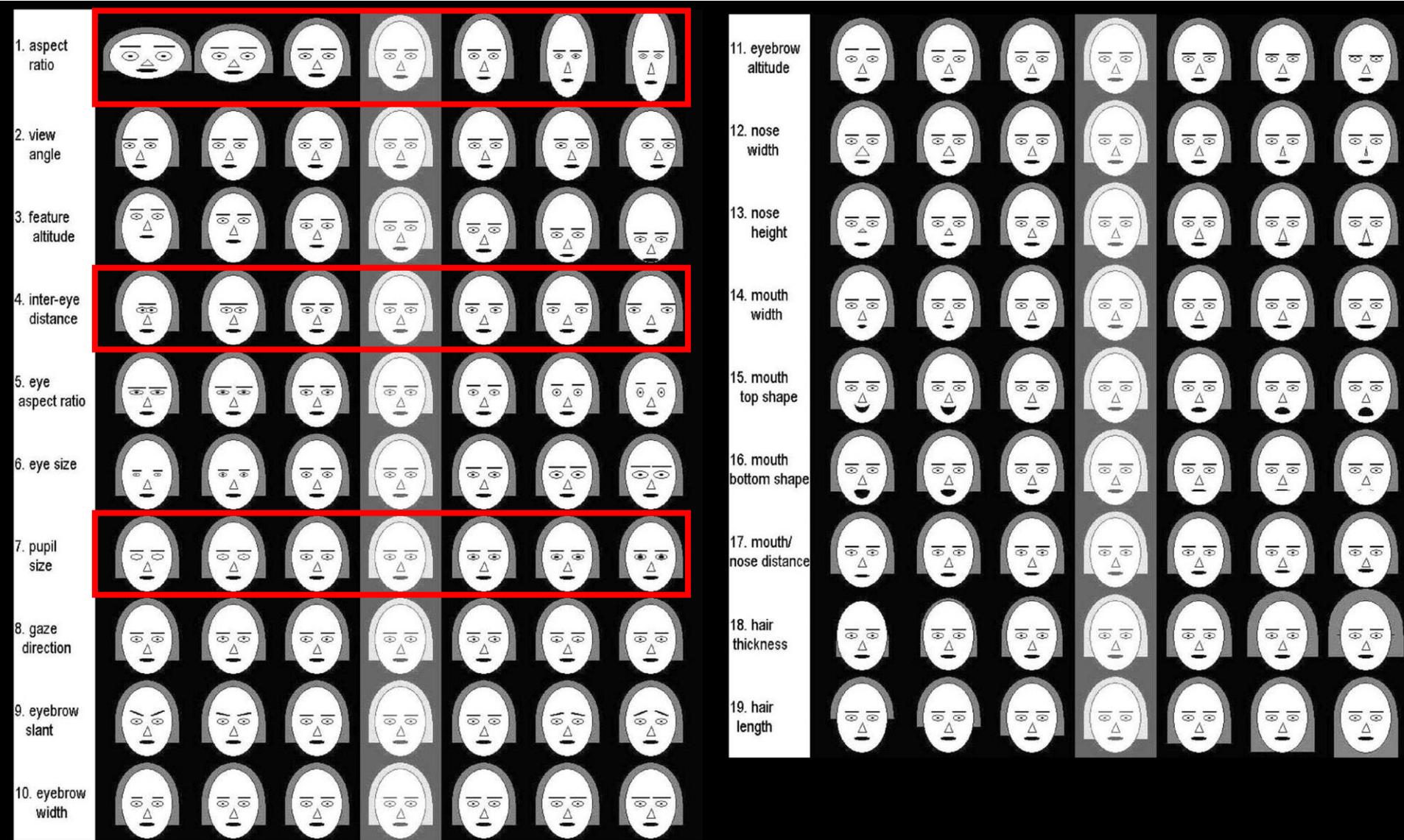
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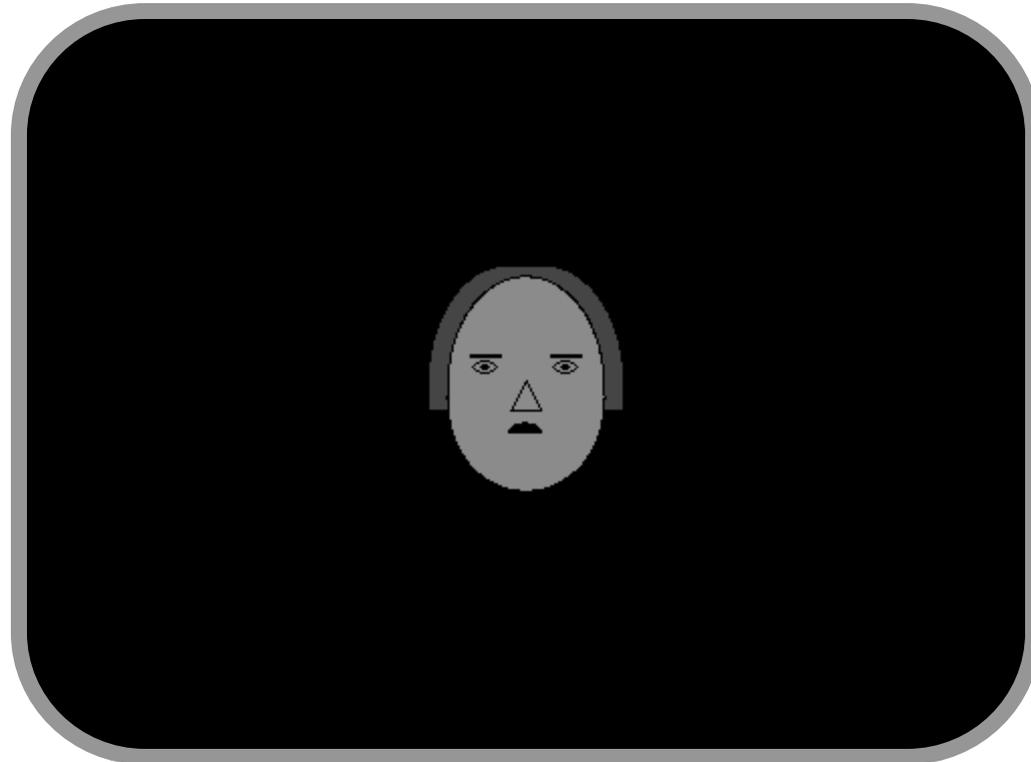
Source: Freiwald, Winrich A., Doris
Y. Tsao, and Margaret S. Livingstone
"A face feature space in the macaque
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12, no. 9 (2009): 1187-1196.

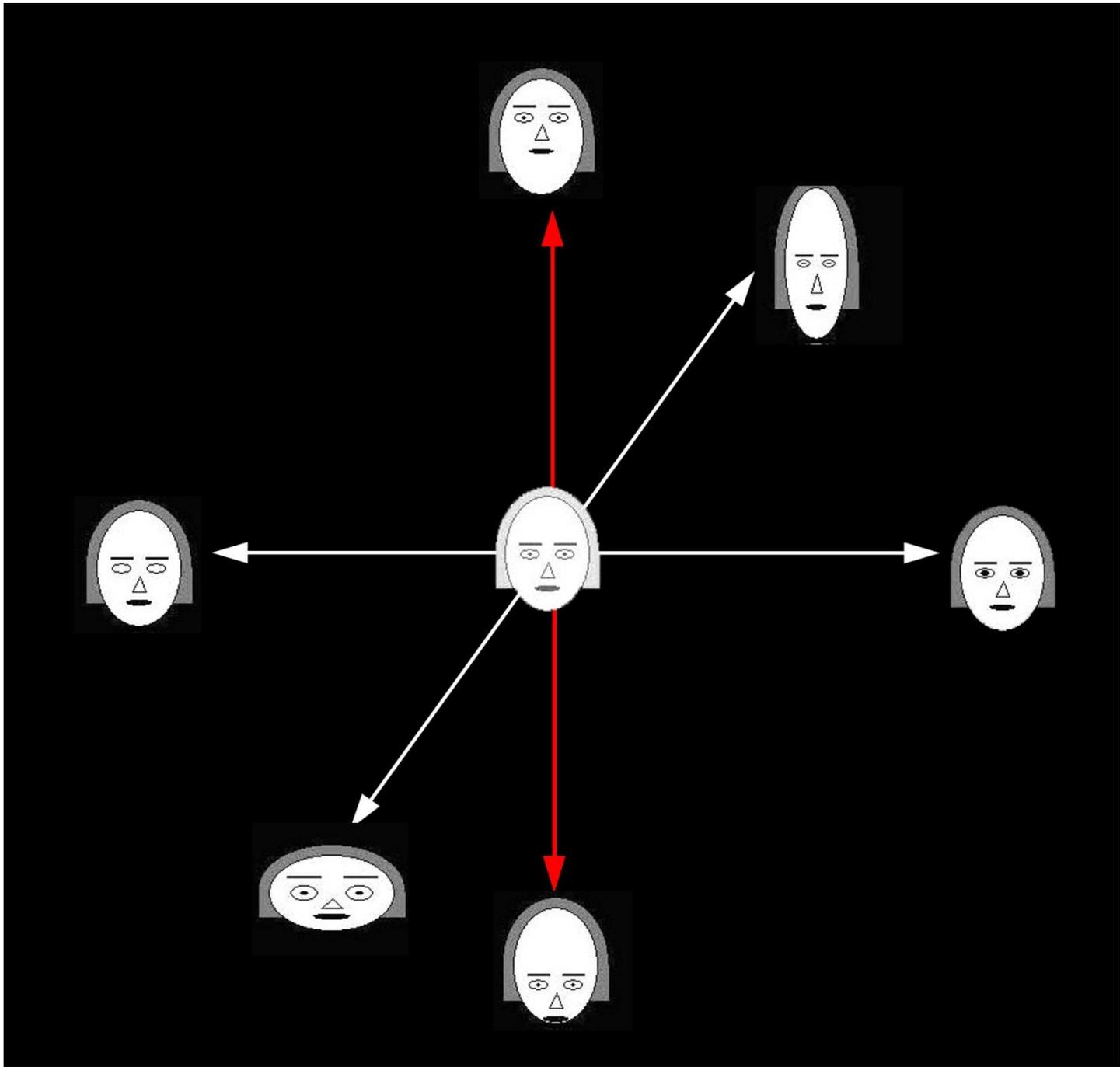
A Parameterized Cartoon Face Space



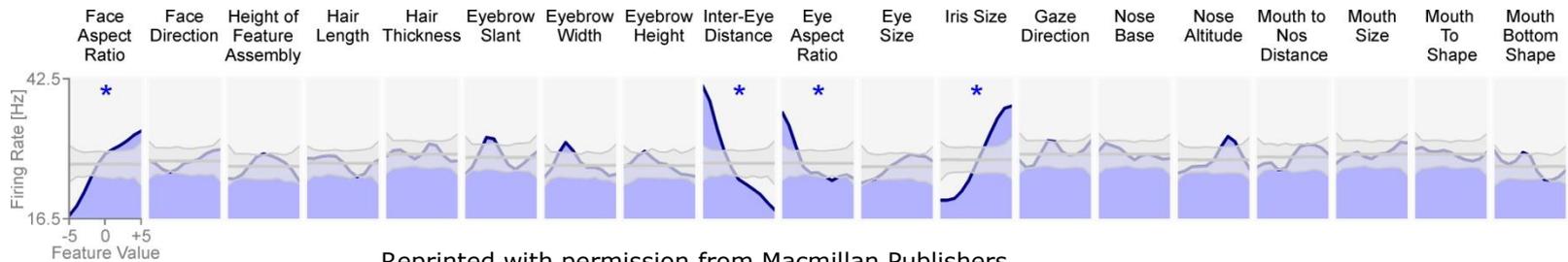
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 Source: Freiwald, Winrich A., Doris Y. Tsao, and Margaret S. Livingstone. "A face feature space in the macaque temporal lobe." *Nature neuroscience* 12, no. 9 (2009): 1187-1196.

A Parameterized Cartoon Face Space

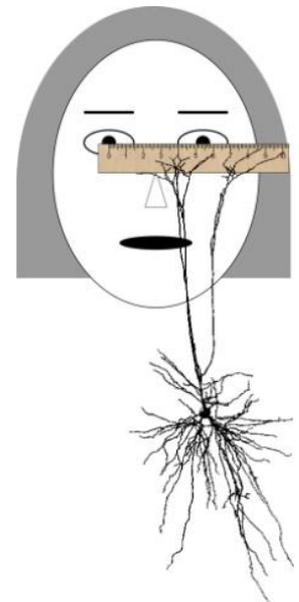
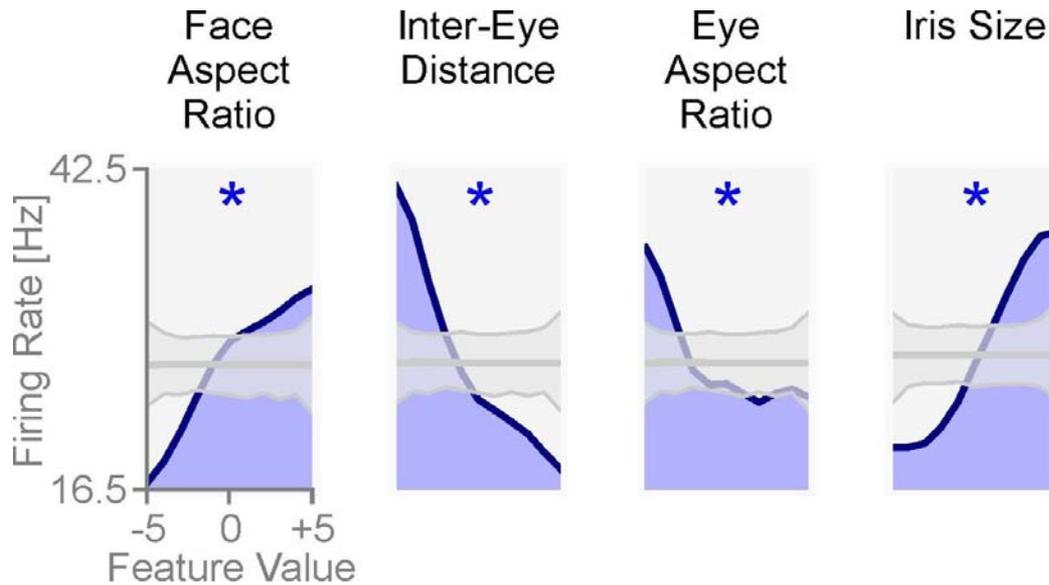




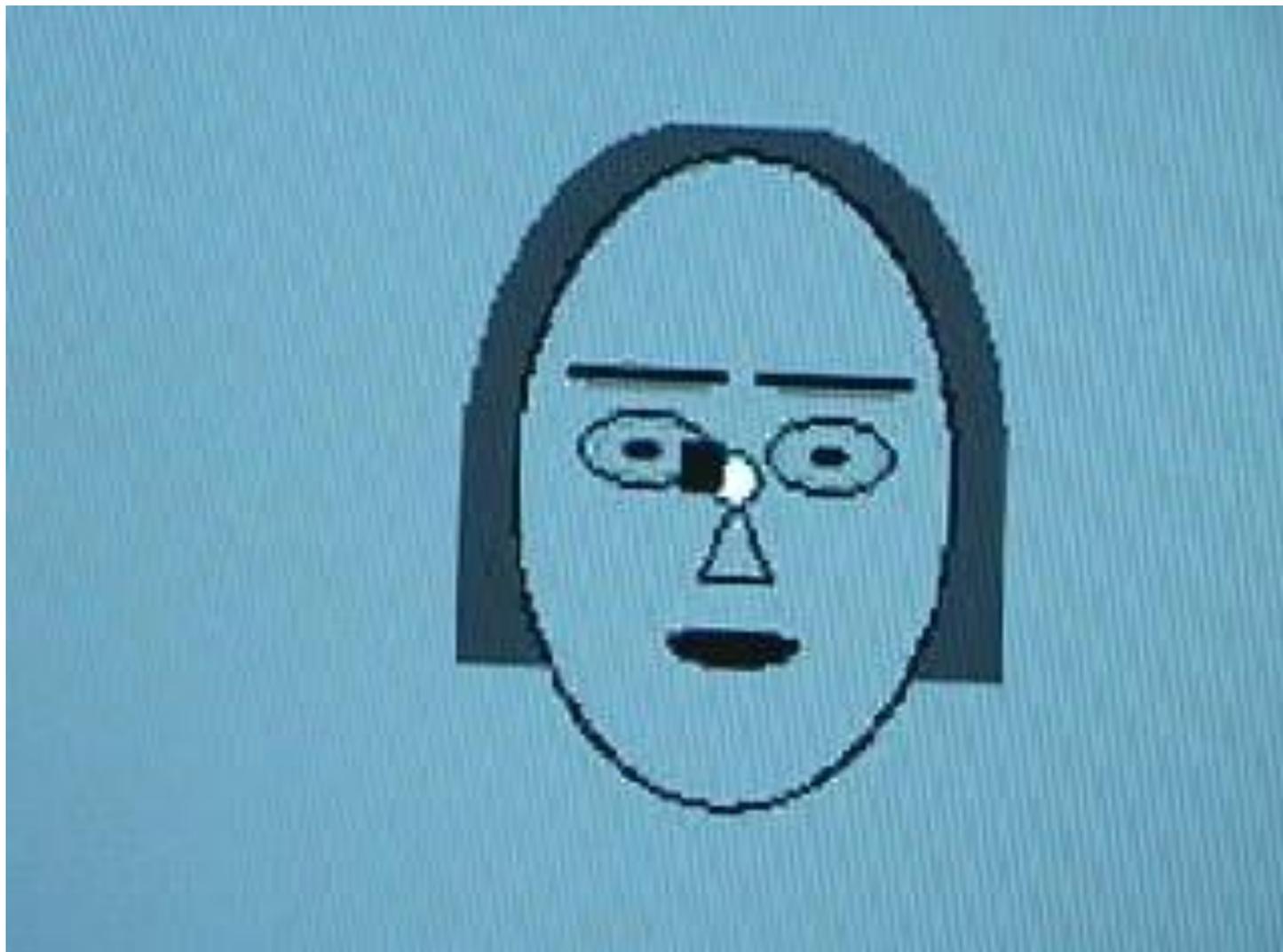
Tuning to Features: an Example Face Cell



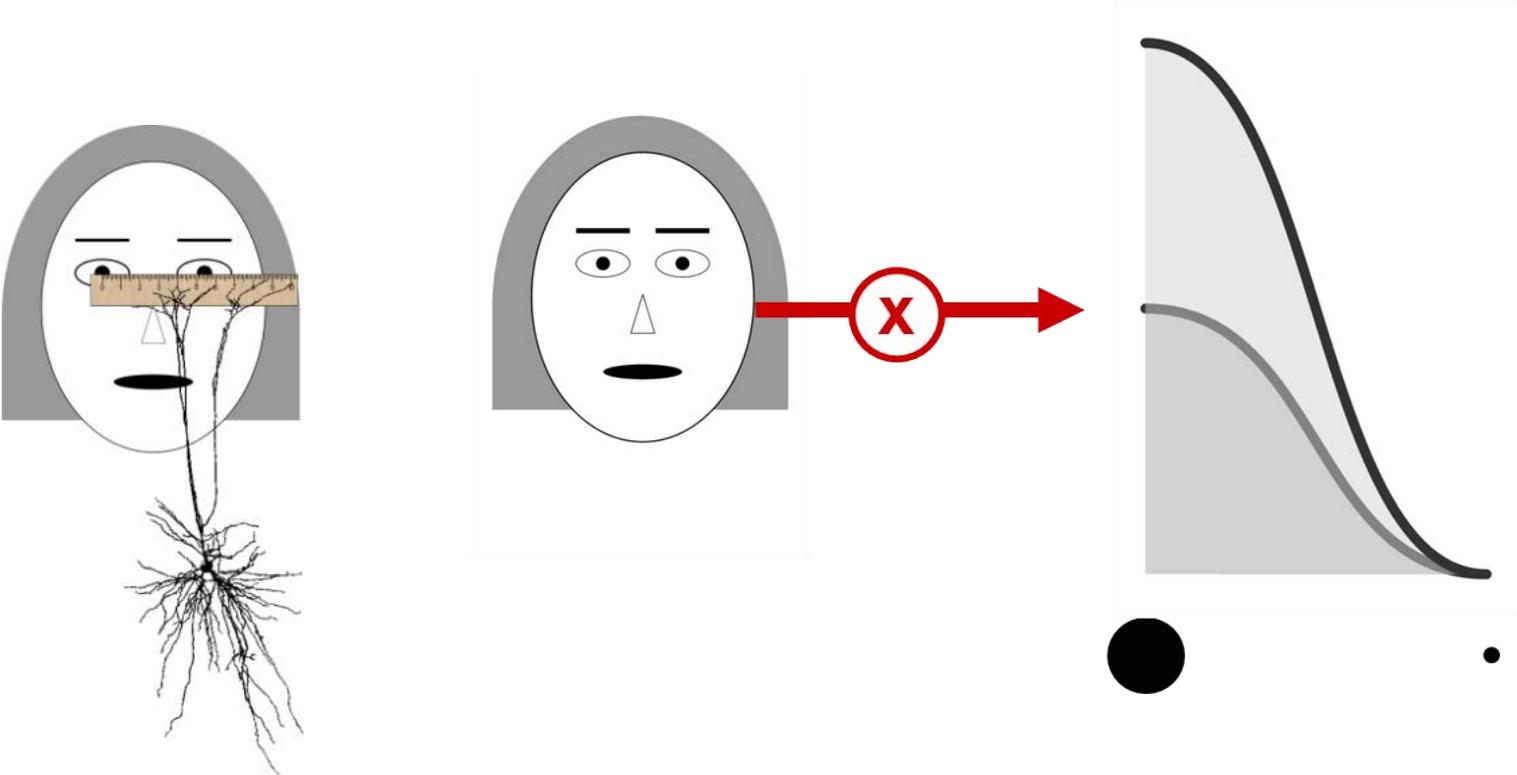
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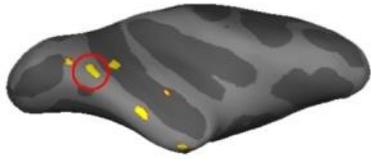


Are features tuned in isolation?



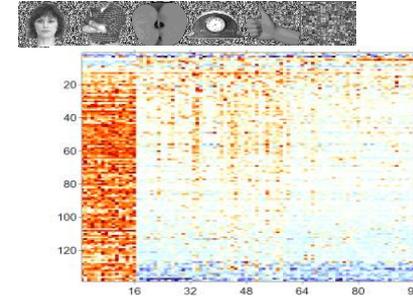
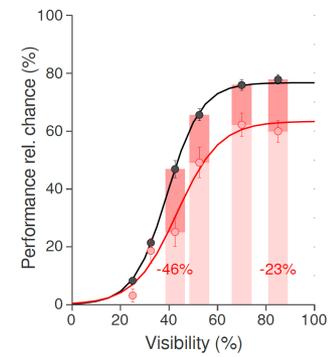
Feature Tuning & Holistic Gain Modulation in the middle face patches



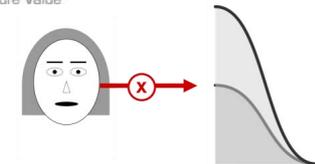
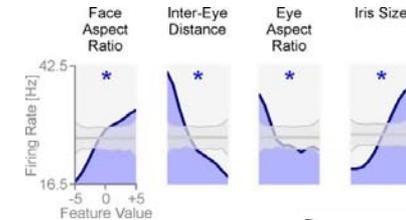


Middle Face Patches

- 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



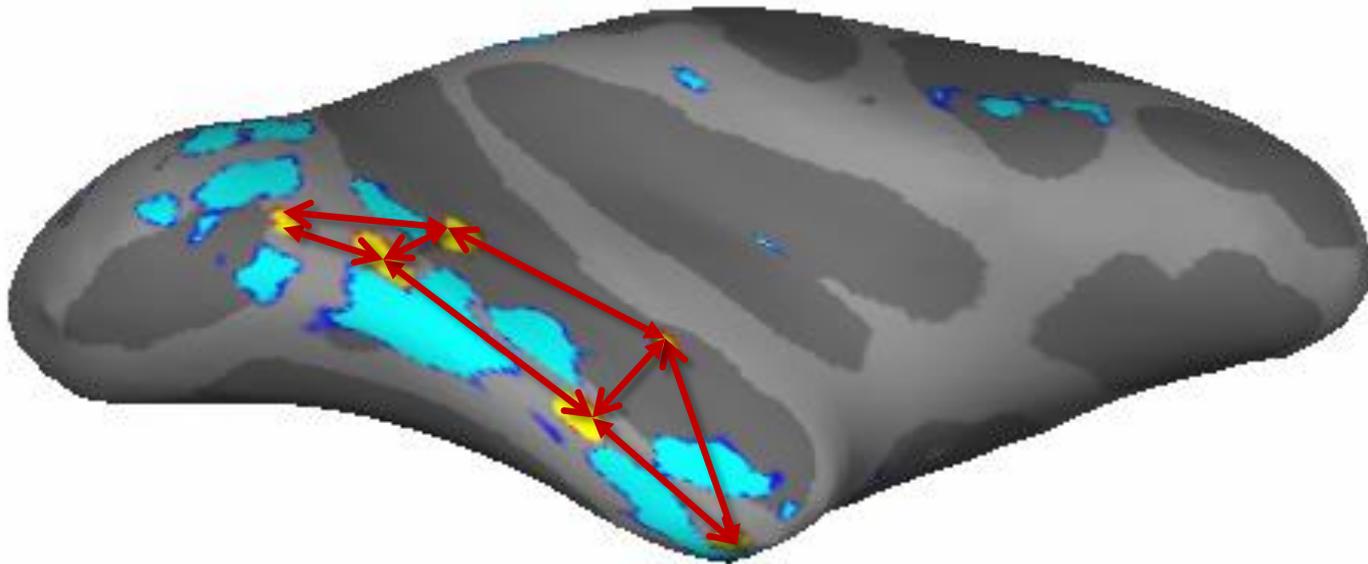
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 Source: Freiwald, Winrich A., Doris Y. Tsao, and Margaret S. Livingstone. "A face feature space in the macaque temporal lobe." *Nature neuroscience* 12, no. 9 (2009): 1187-1196.





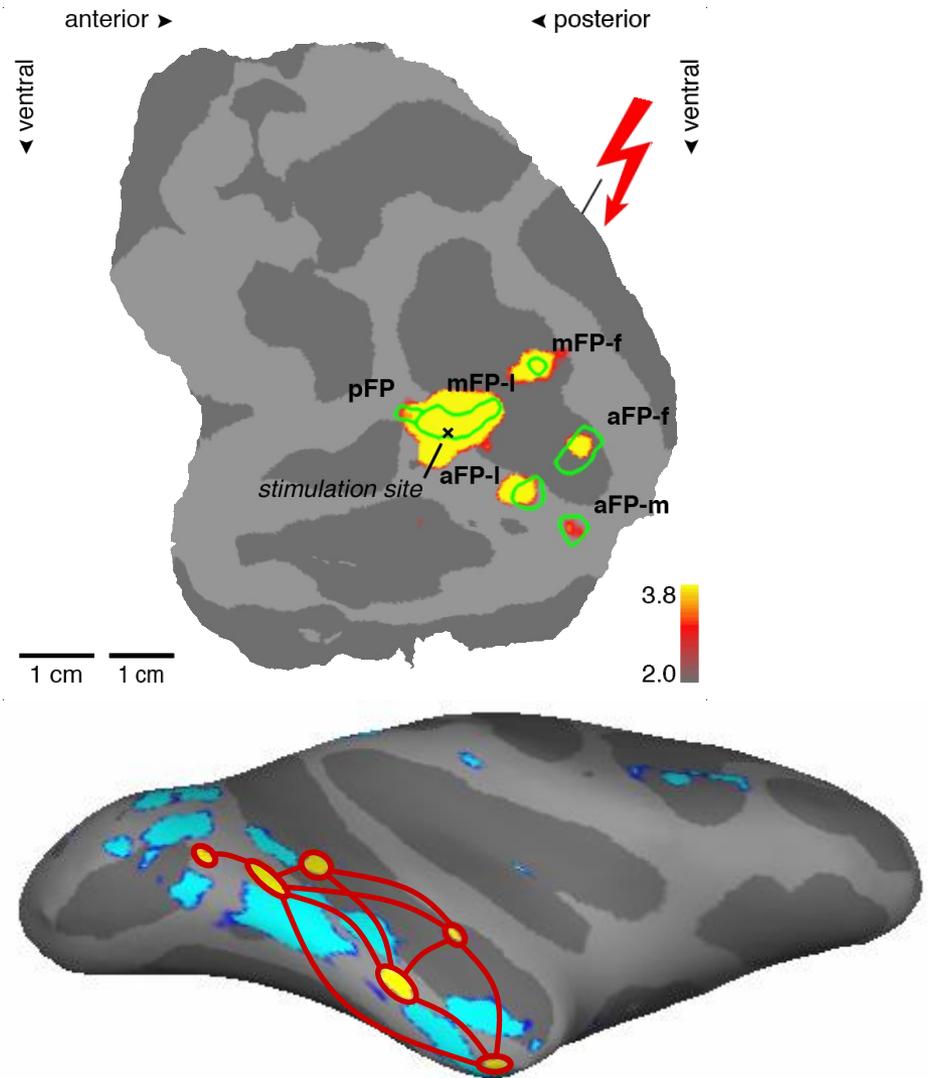
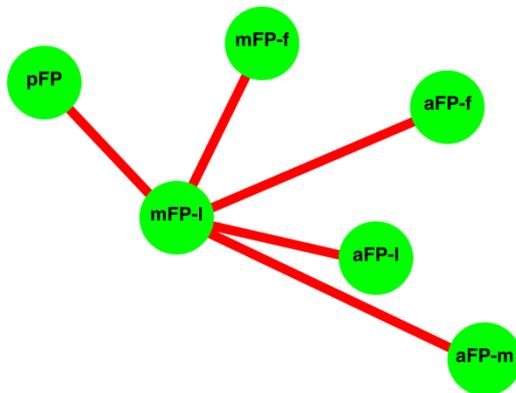
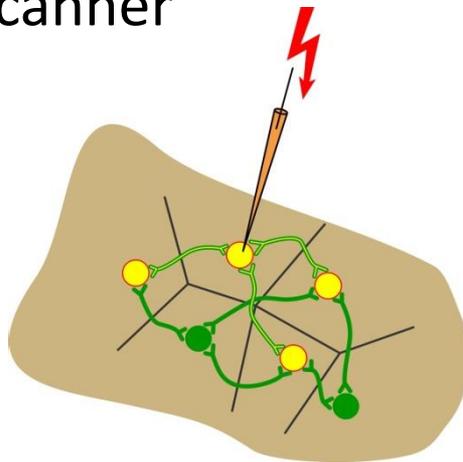
The macaque face processing system: determining connectivity

Sebastian Möller

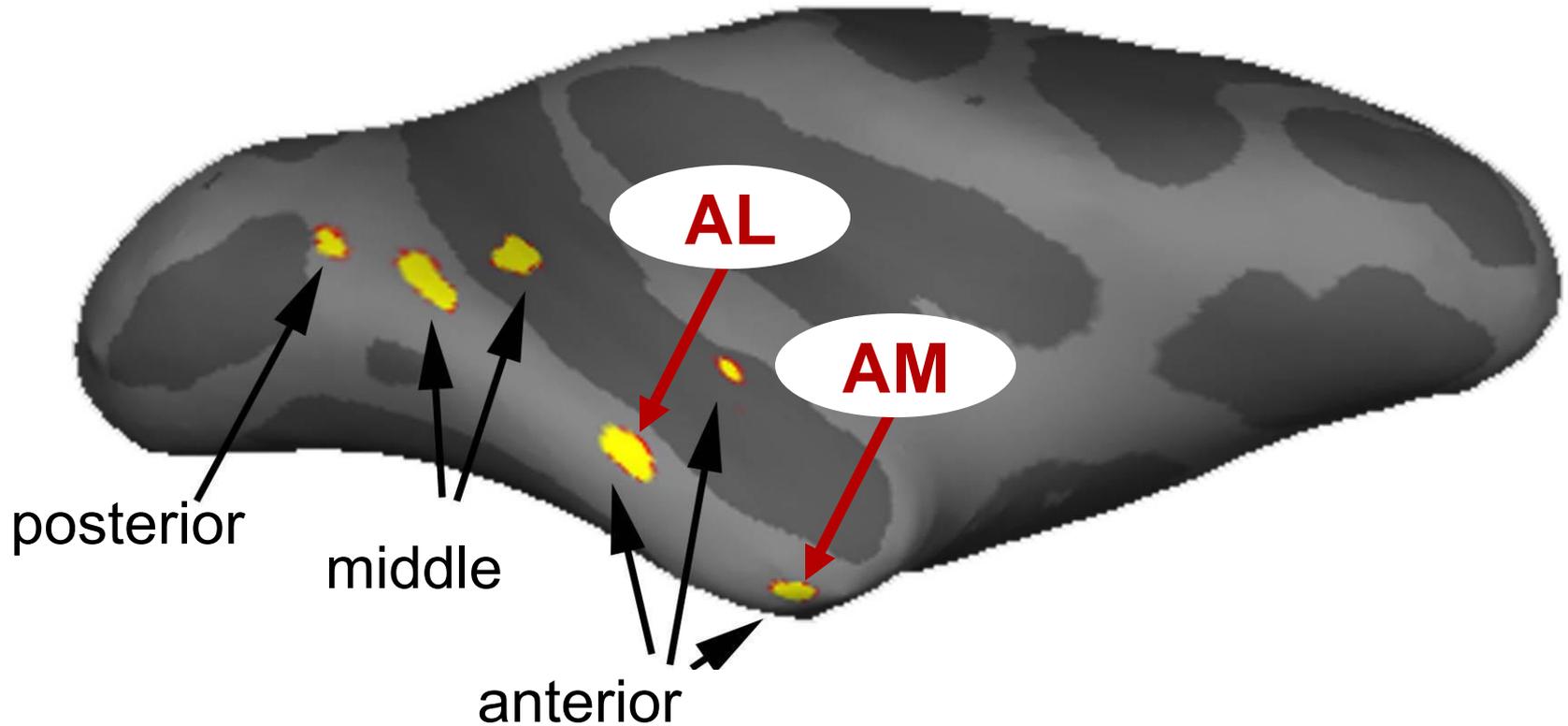


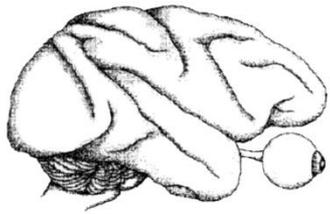
The macaque face processing system: determining connectivity

electrical stimulation inside
the MR scanner

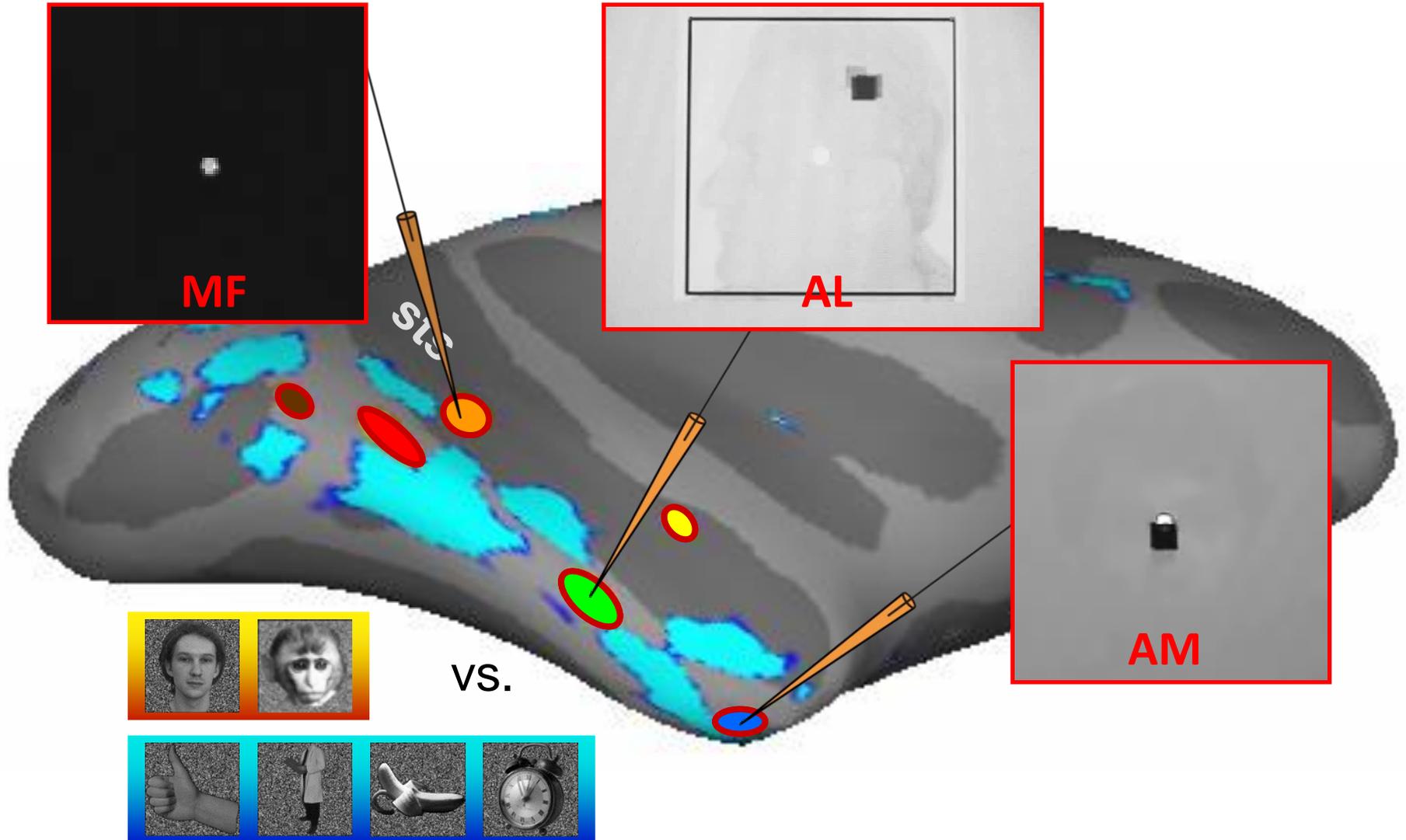


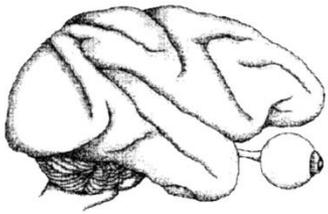
How does face selectivity develop along the face patch hierarchy?





Electrophysiological Recordings in Three Face Patches





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

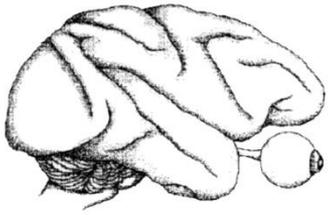
Affine Transformations



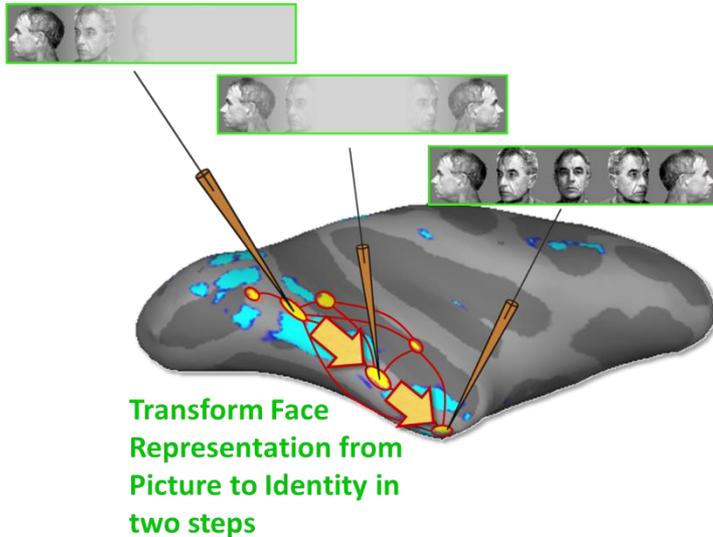
Non-affine Transformations



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

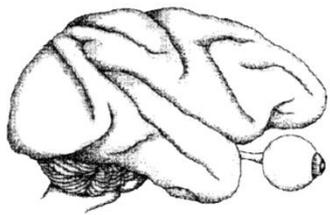


Modular Architecture
3-Level Processing Hierarchy

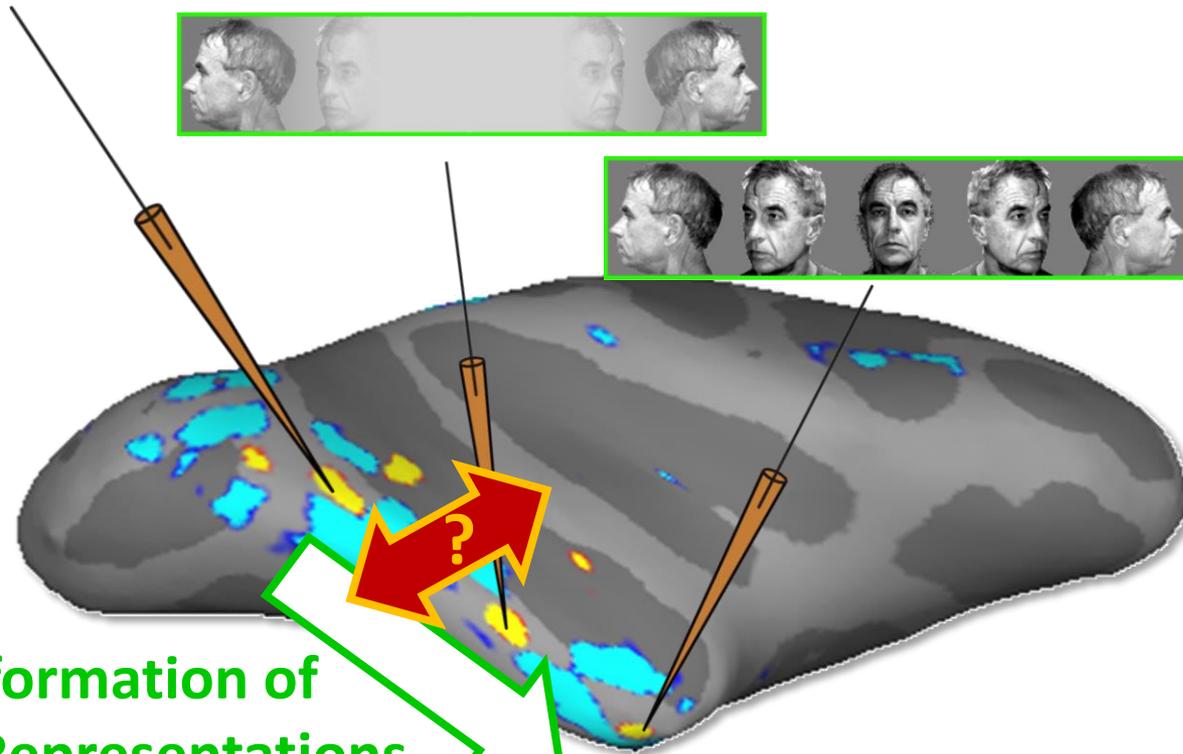
Level 1: Face Filter
Level 3: Identification
+ Hebbian Learning Rule

=

Level 3: Invariance
Level 2: Mirror-Symmetry



The macaque face processing system: transformations



Transformation of
Face Representations
from Picture to Identity

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.

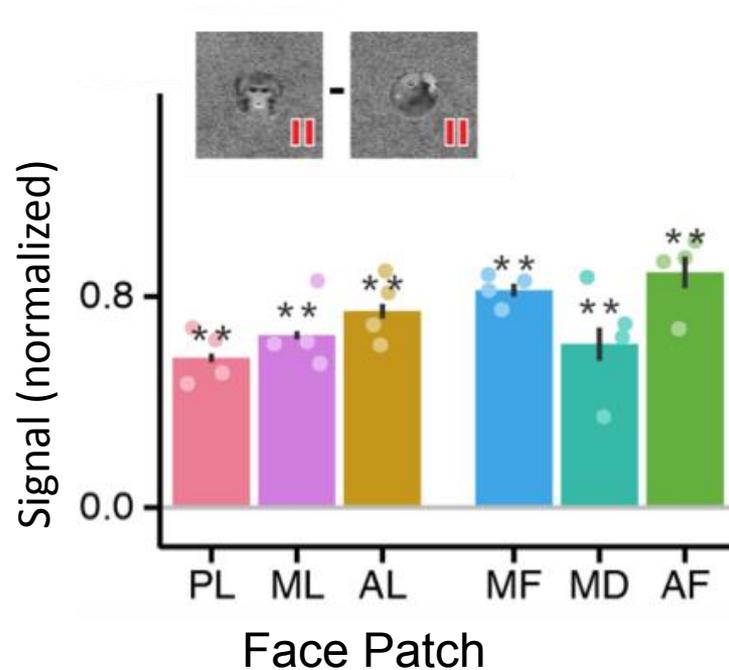
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The macaque face processing system: sensitivity to stimulus motion

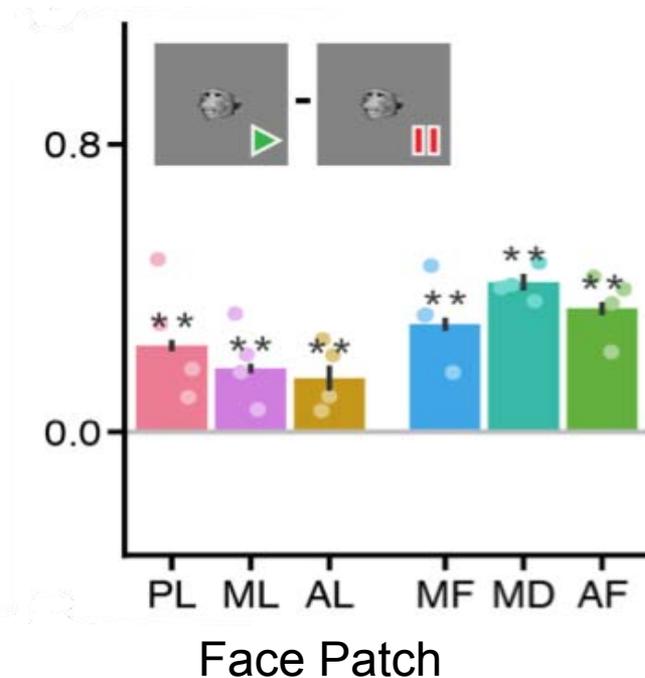


The macaque face processing system: Sensitivity to stimulus motion

Face Form-Selective



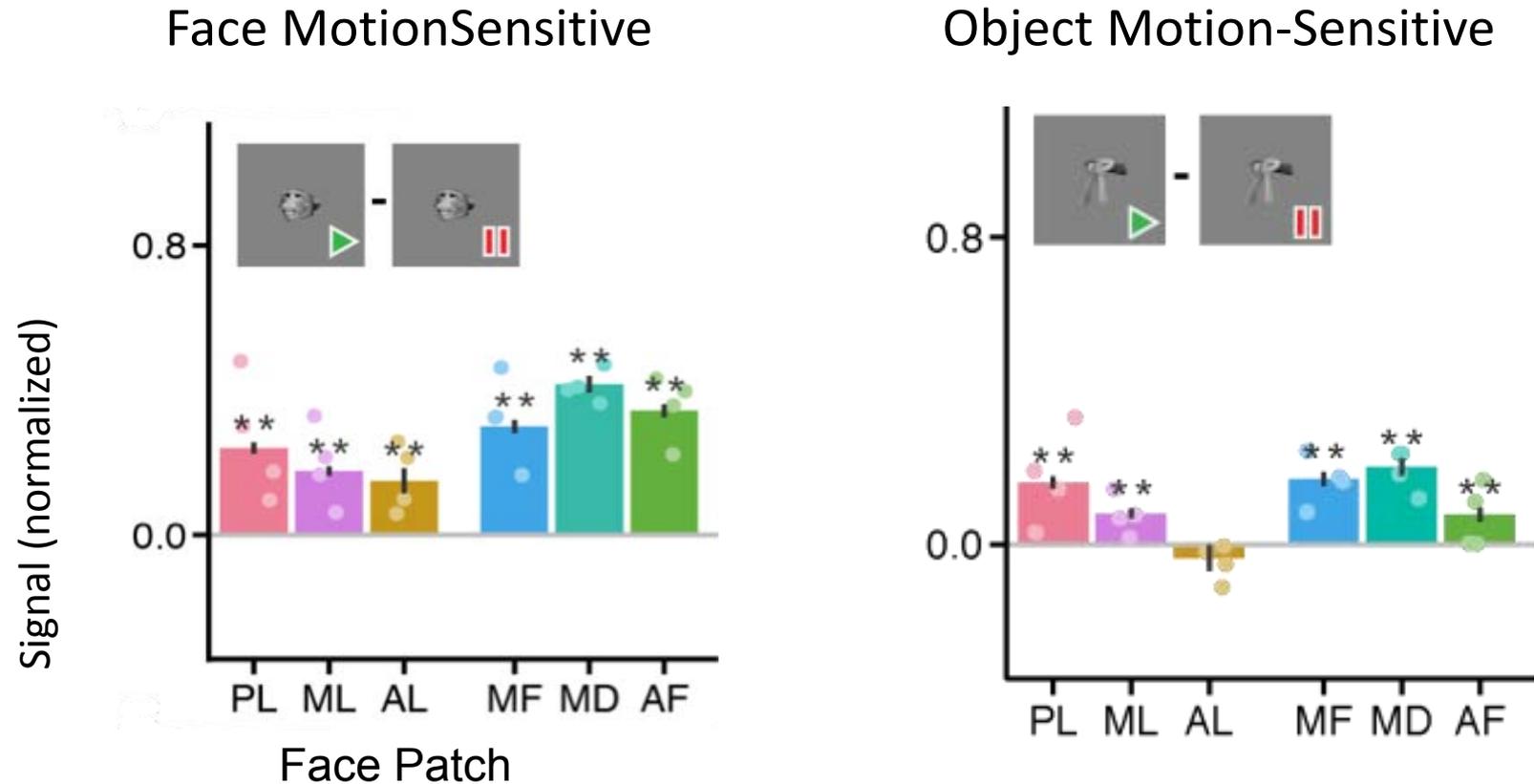
Face Motion-Sensitive



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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.

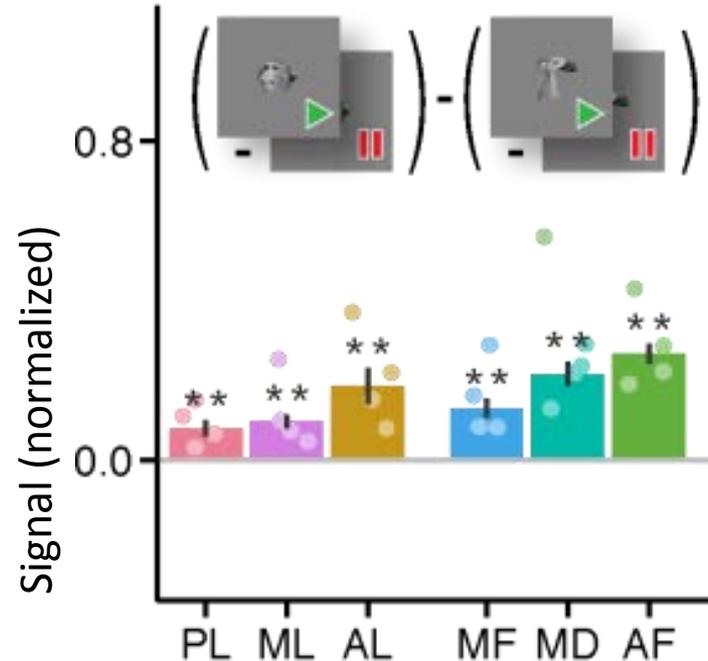
The macaque face processing system: Sensitivity to stimulus motion



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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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Moving



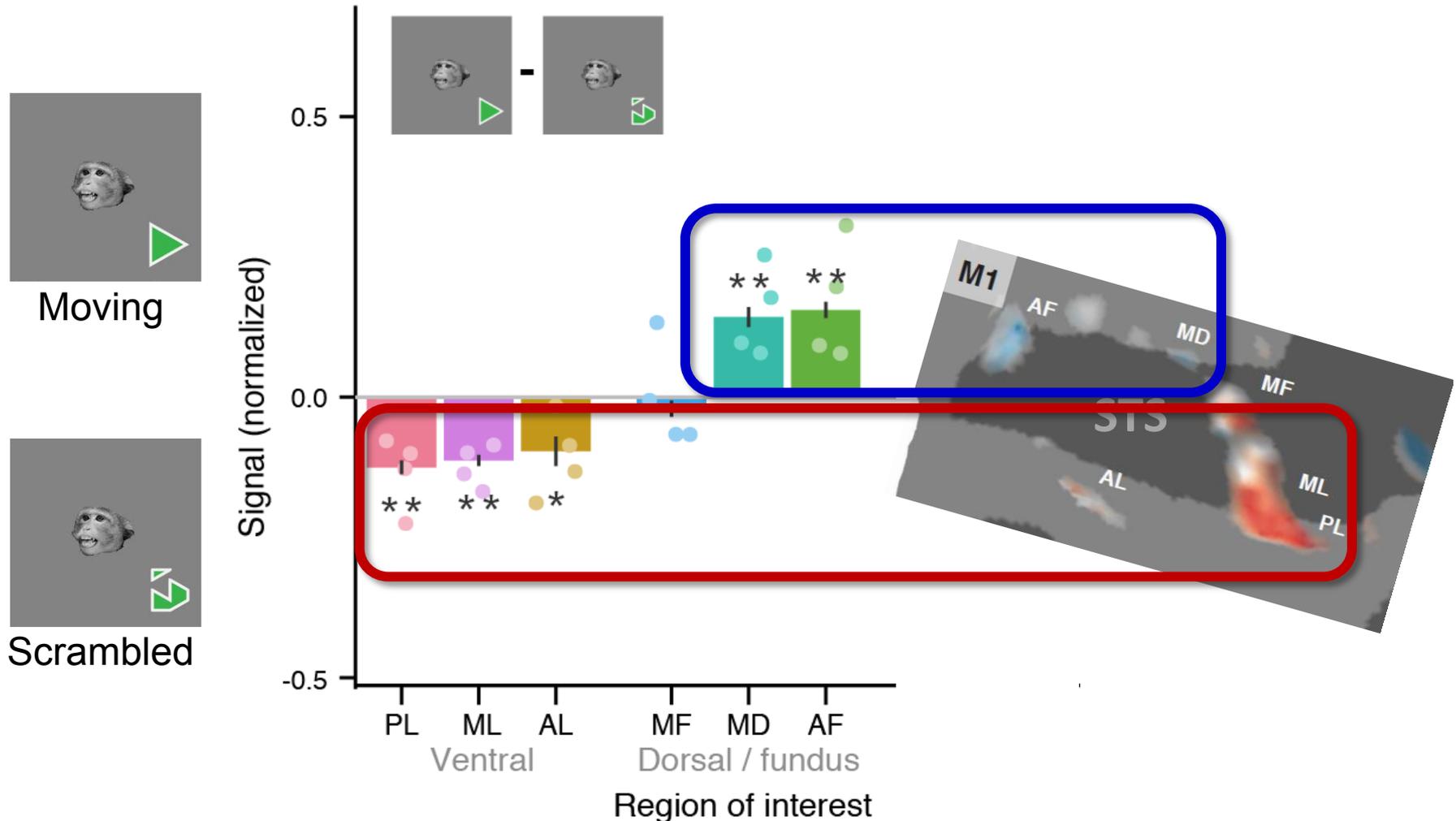
>

Still



Motion?
Image content?
Update frequency?

The macaque face processing system: A new Functional Division



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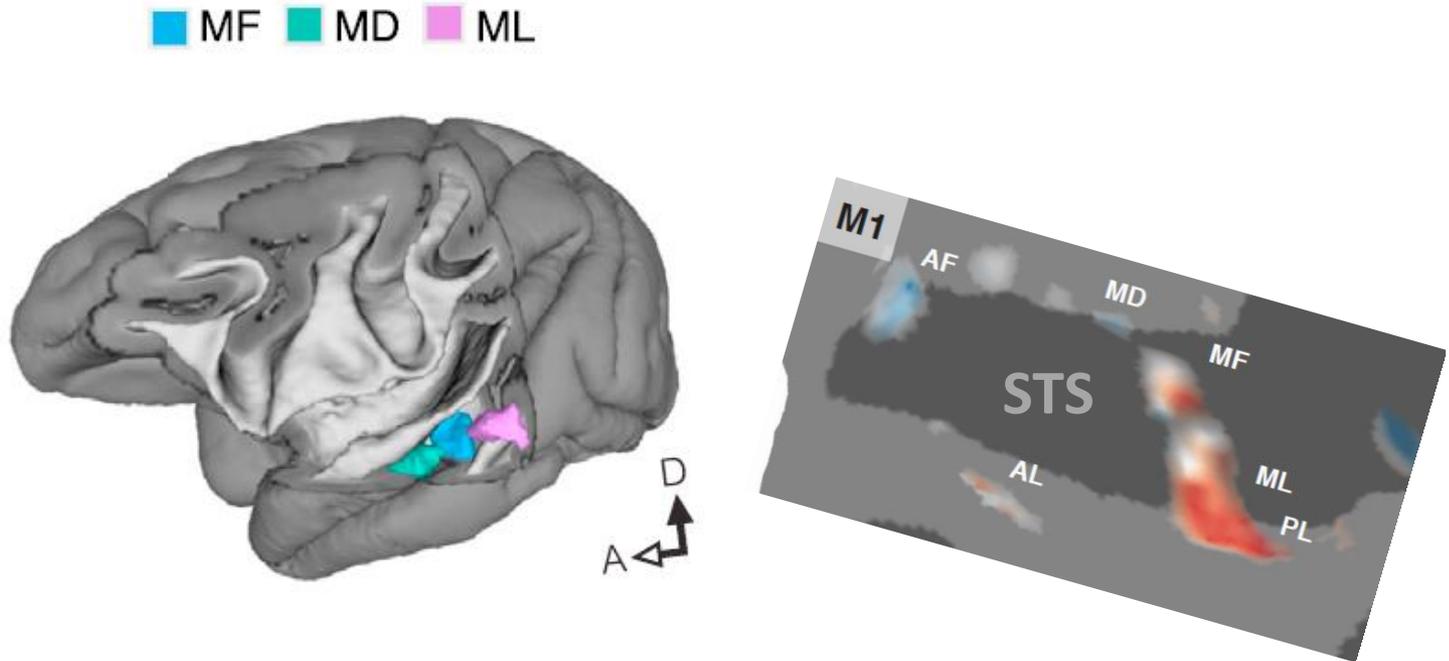
The macaque face processing system: A new Functional Division



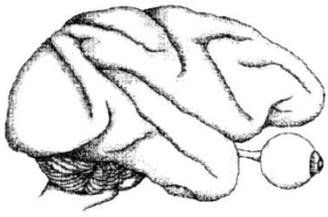
Moving



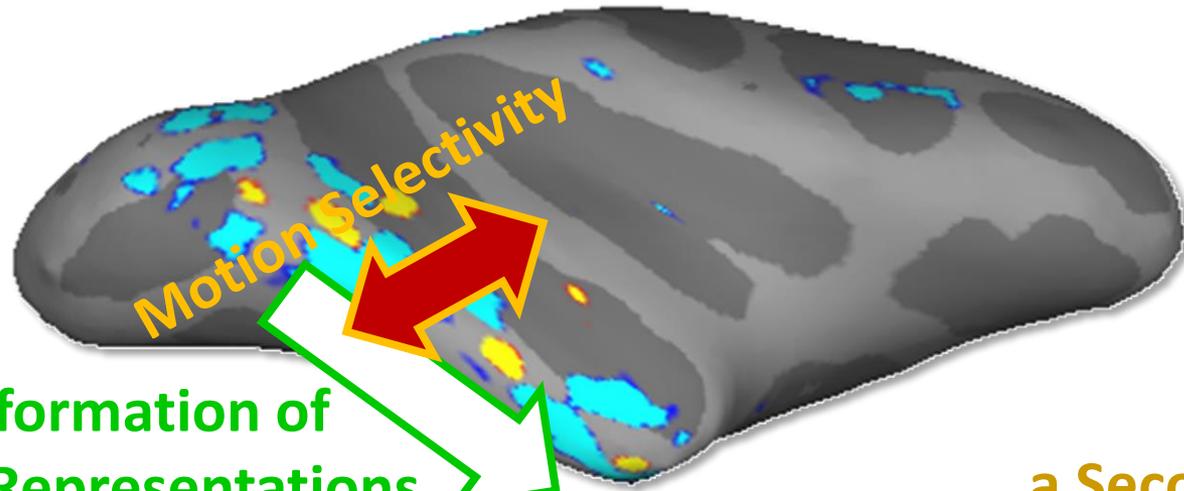
Scrambled



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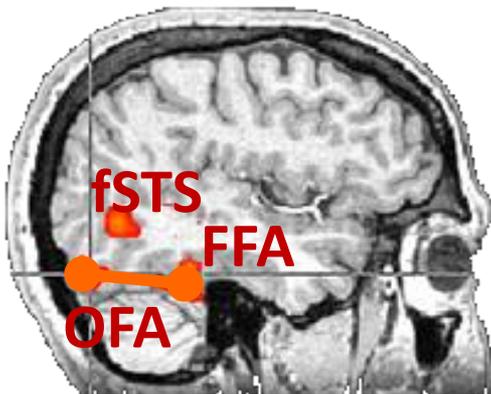


The macaque face processing system: two axes of functional specialization



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

**a Second
Face-Processing System**

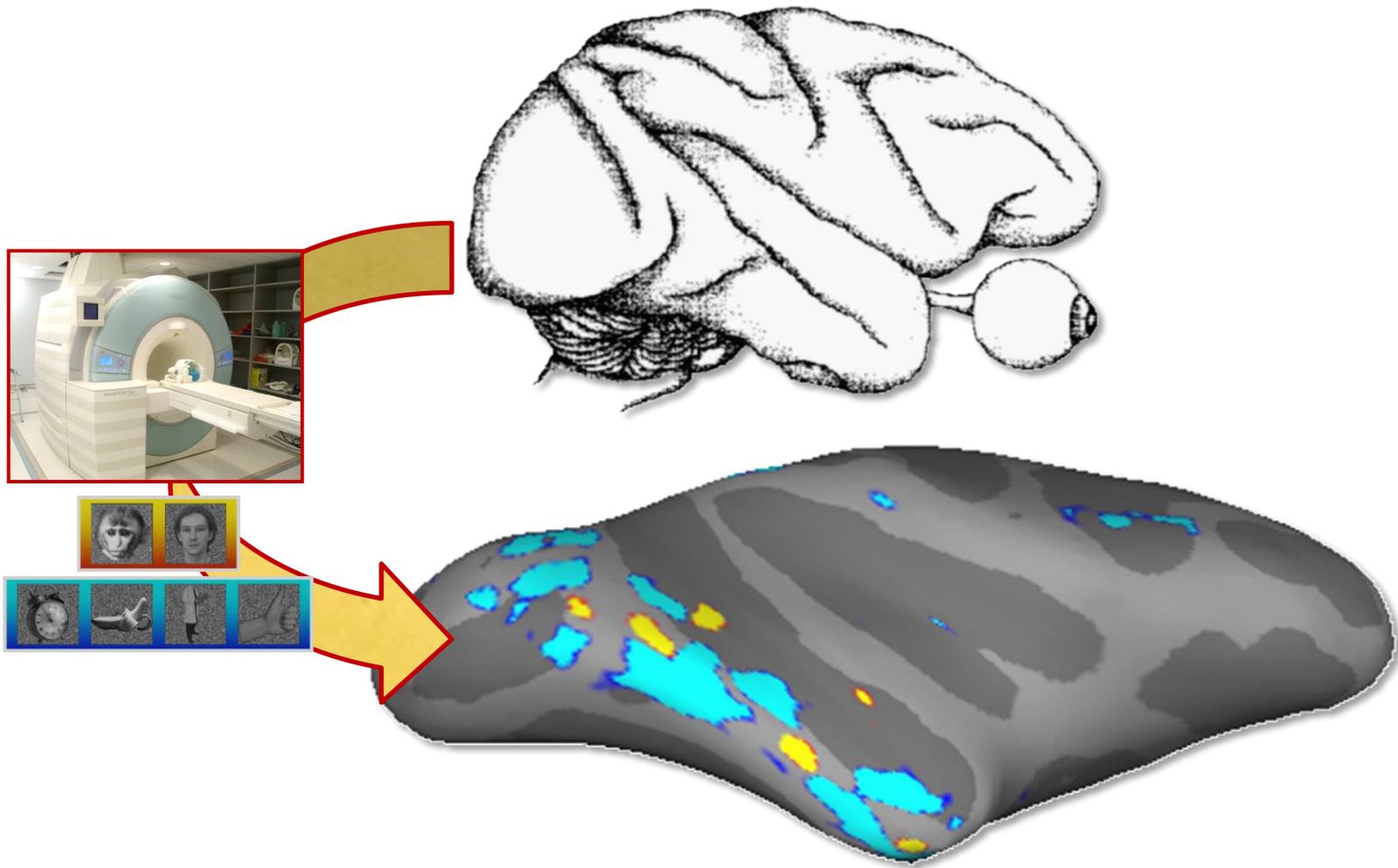


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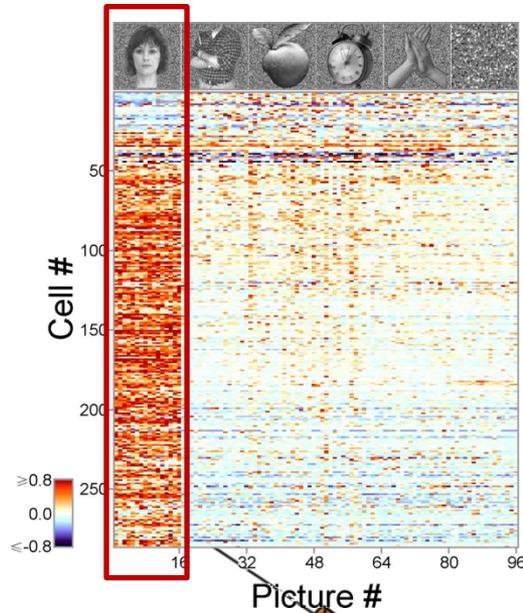
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The Neural Circuits of Face Processing

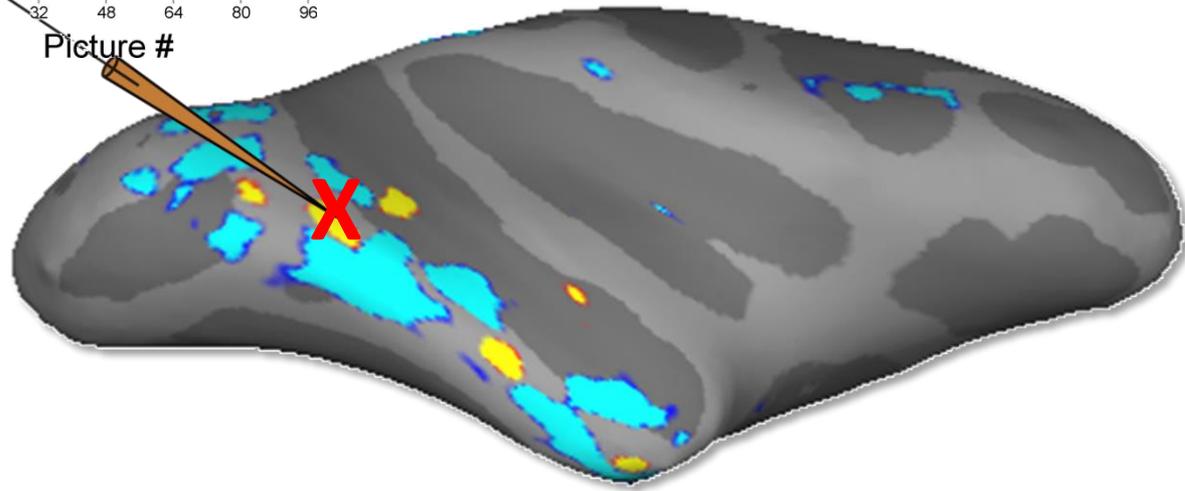


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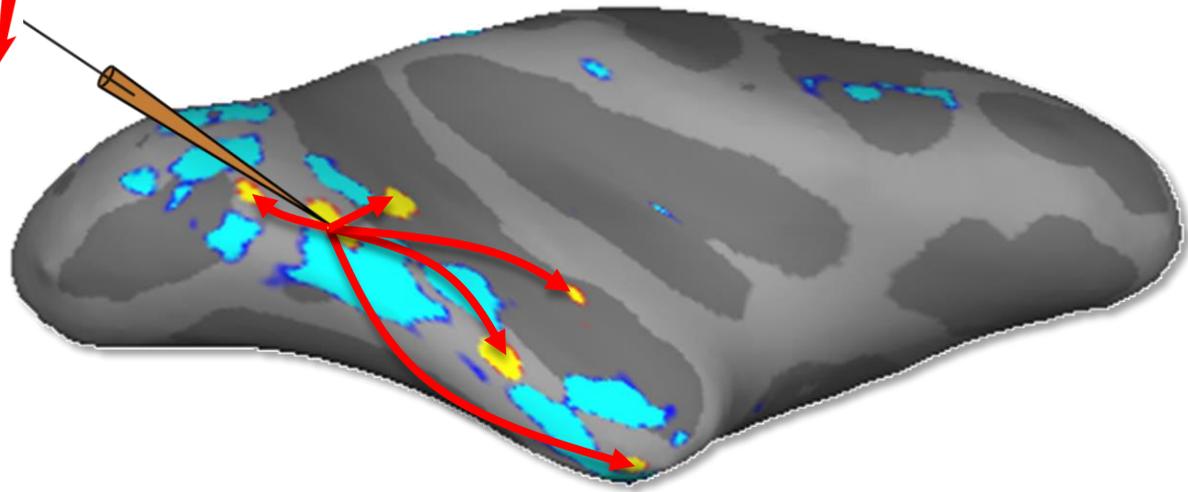
The Neural Circuits of Face Processing



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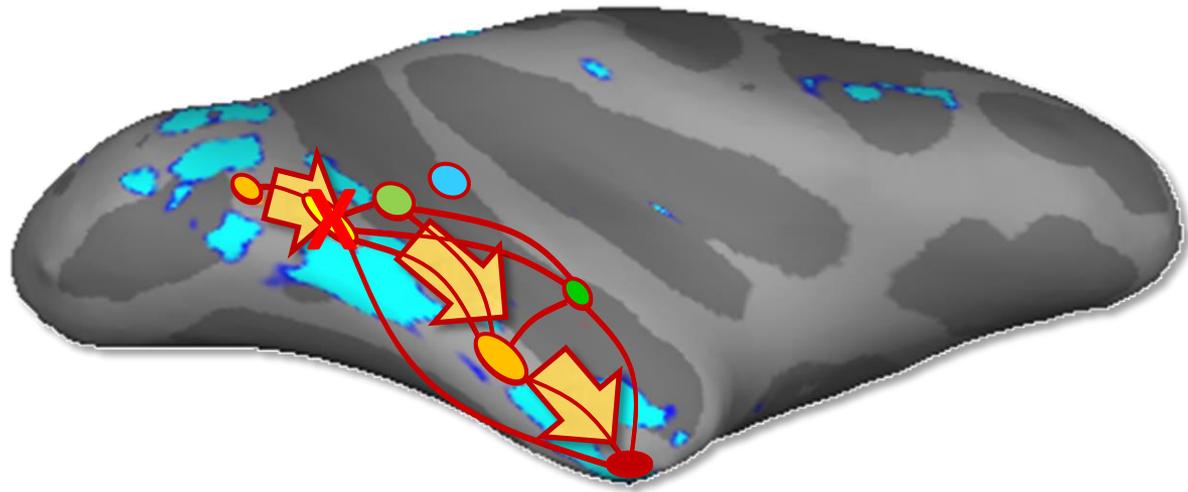


The Neural Circuits of Face Processing



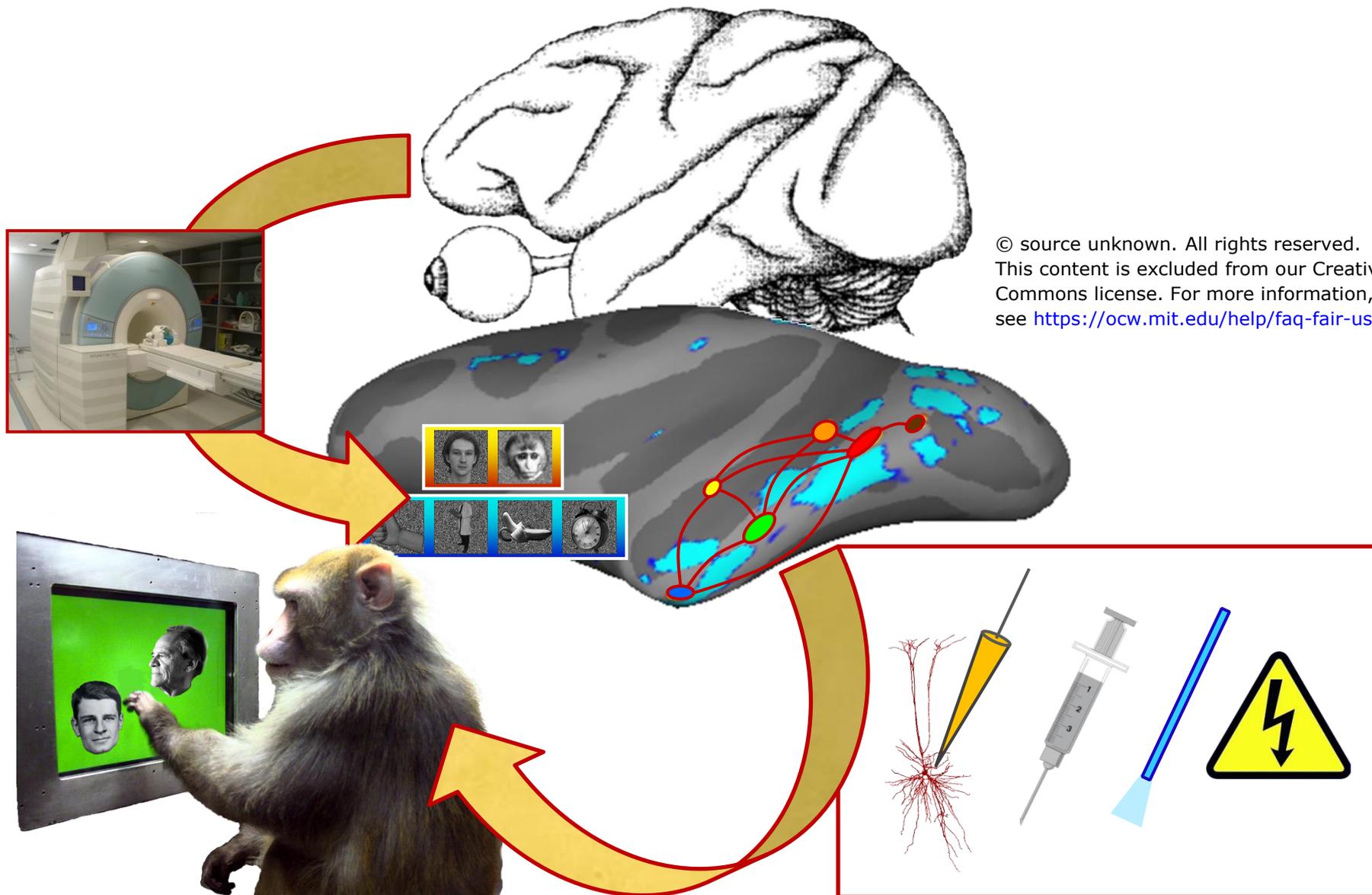
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The Neural Circuits of Face Processing



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Neural Circuit Analysis



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