Does the prefrontal cortex play an essential role in consciousness? Insights from intracranial stimulation of the human brain

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Localist vs cognitivist theories of consciousness

Global workspace theories

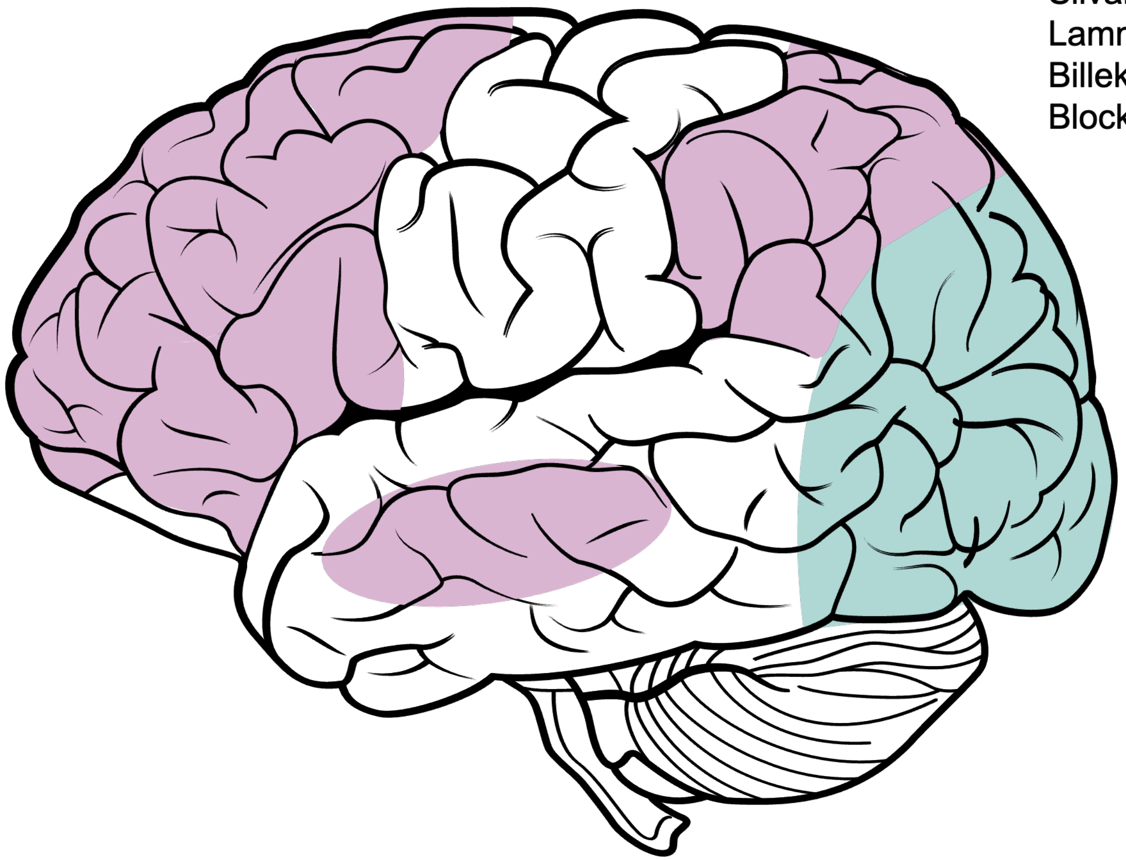
Baars (1993)
Dehaene (2014)
Mashour et al. (2020)

Higher order theories

Rosenthal (2011)
Brown et al. (2015)
Lau (2019)

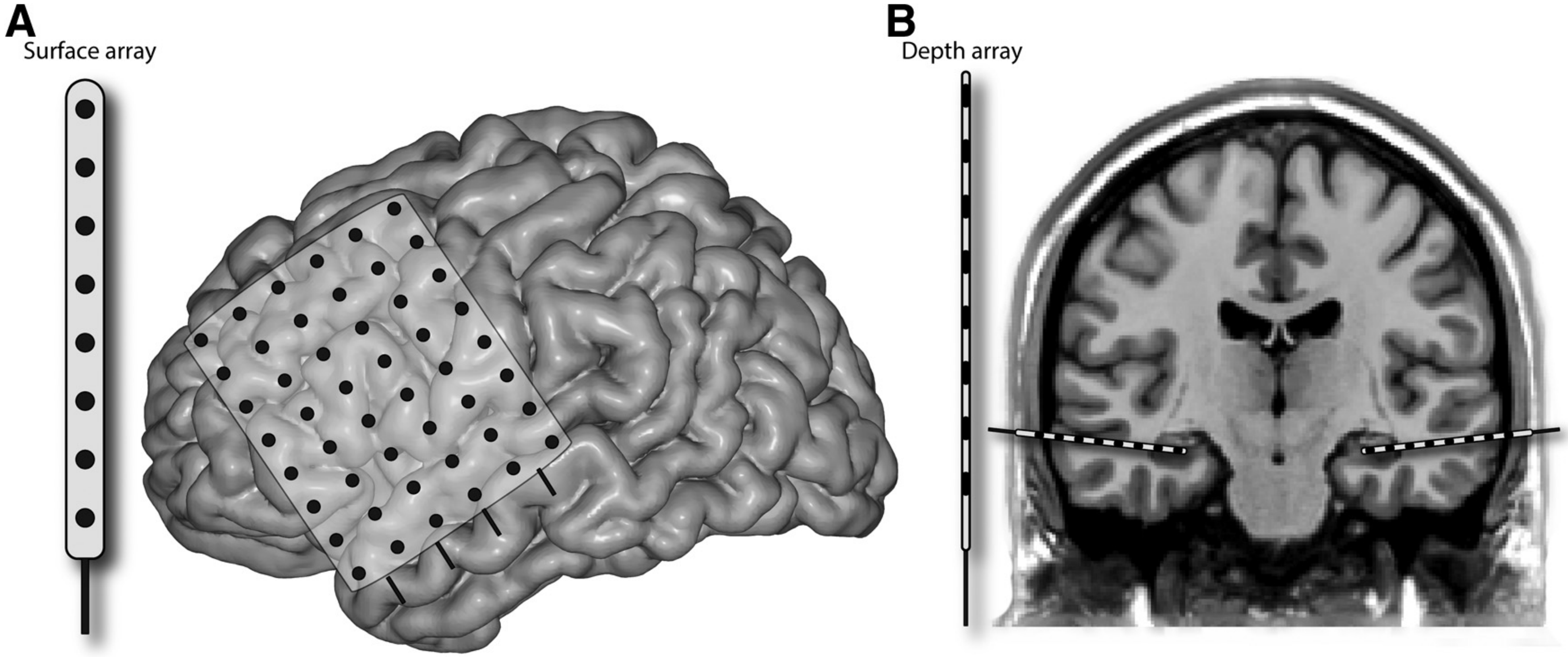
Recurrent activatior theories

Silvanto et al. (2005)
Lamme (2014)
Billeke et al. (2017)
Block (2019)



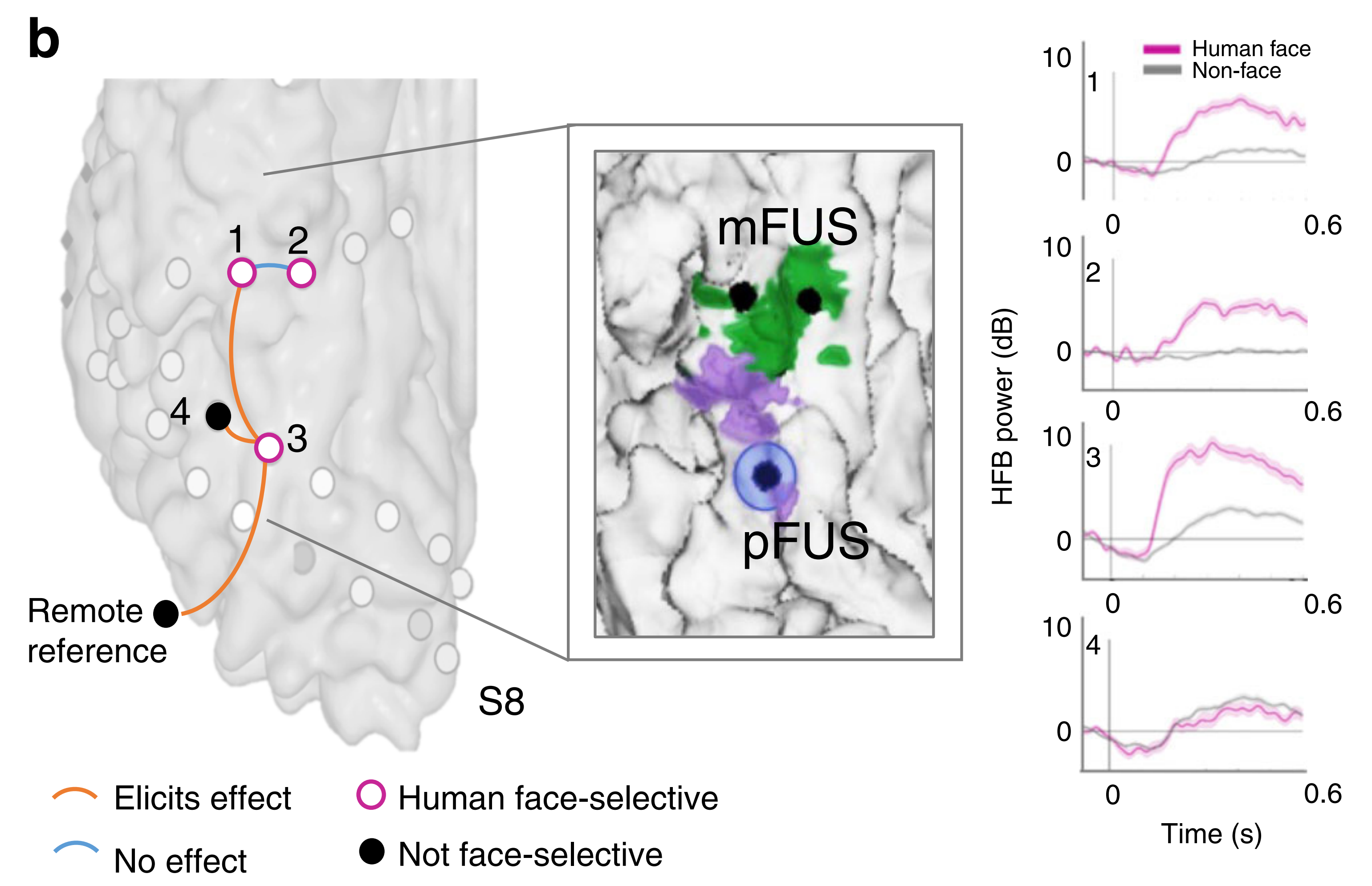
Boly et al., 2017; Odegaard et al., 2017; Block, 2019; Melloni et al., 2021

Intracranial electrical stimulation (iES)



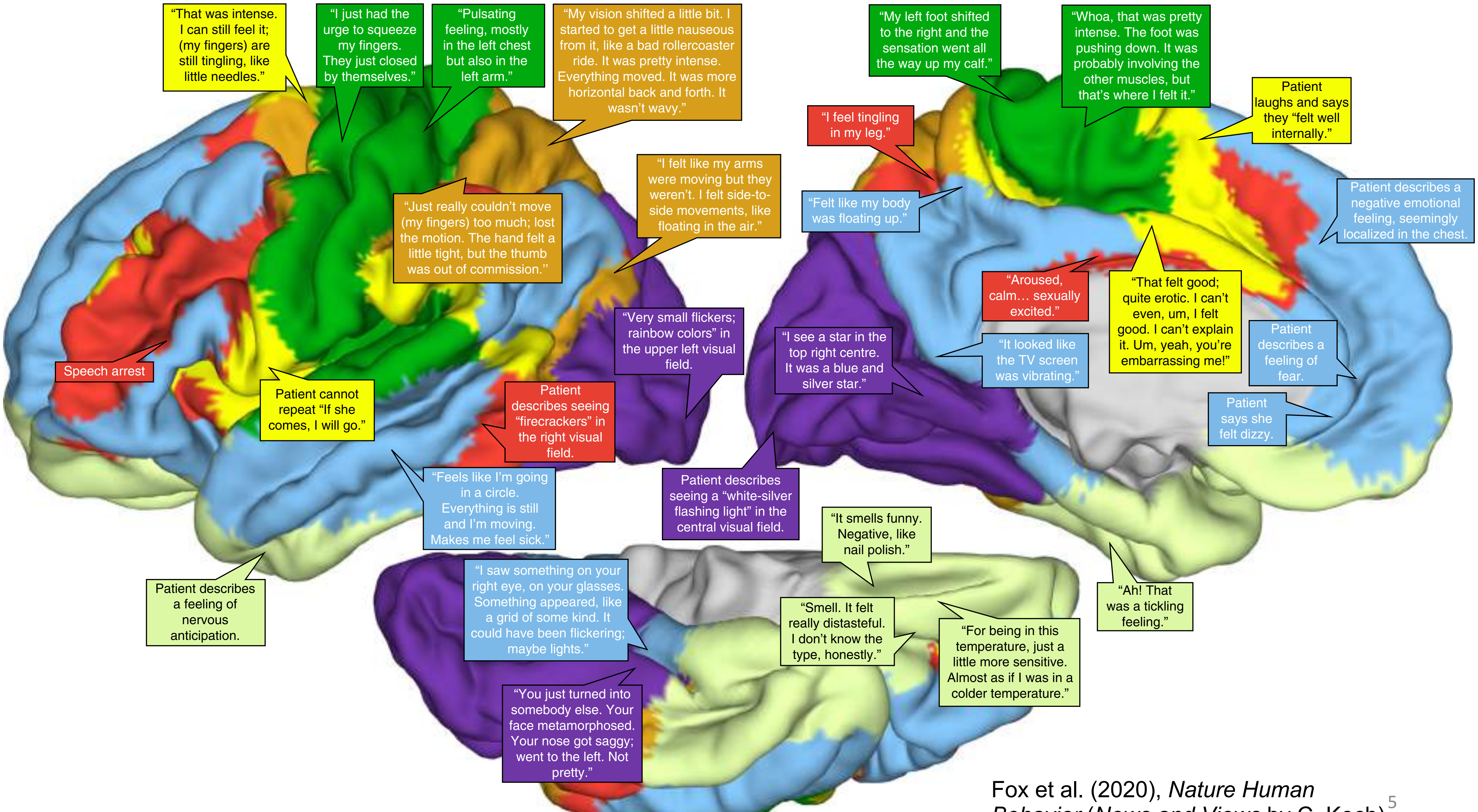
Raccah, Block, & Fox (2021) *JNeuro*

Intracranial electrical stimulation (iES)



Schrouff, Raccah, et al. (2020), *Nature Comm*

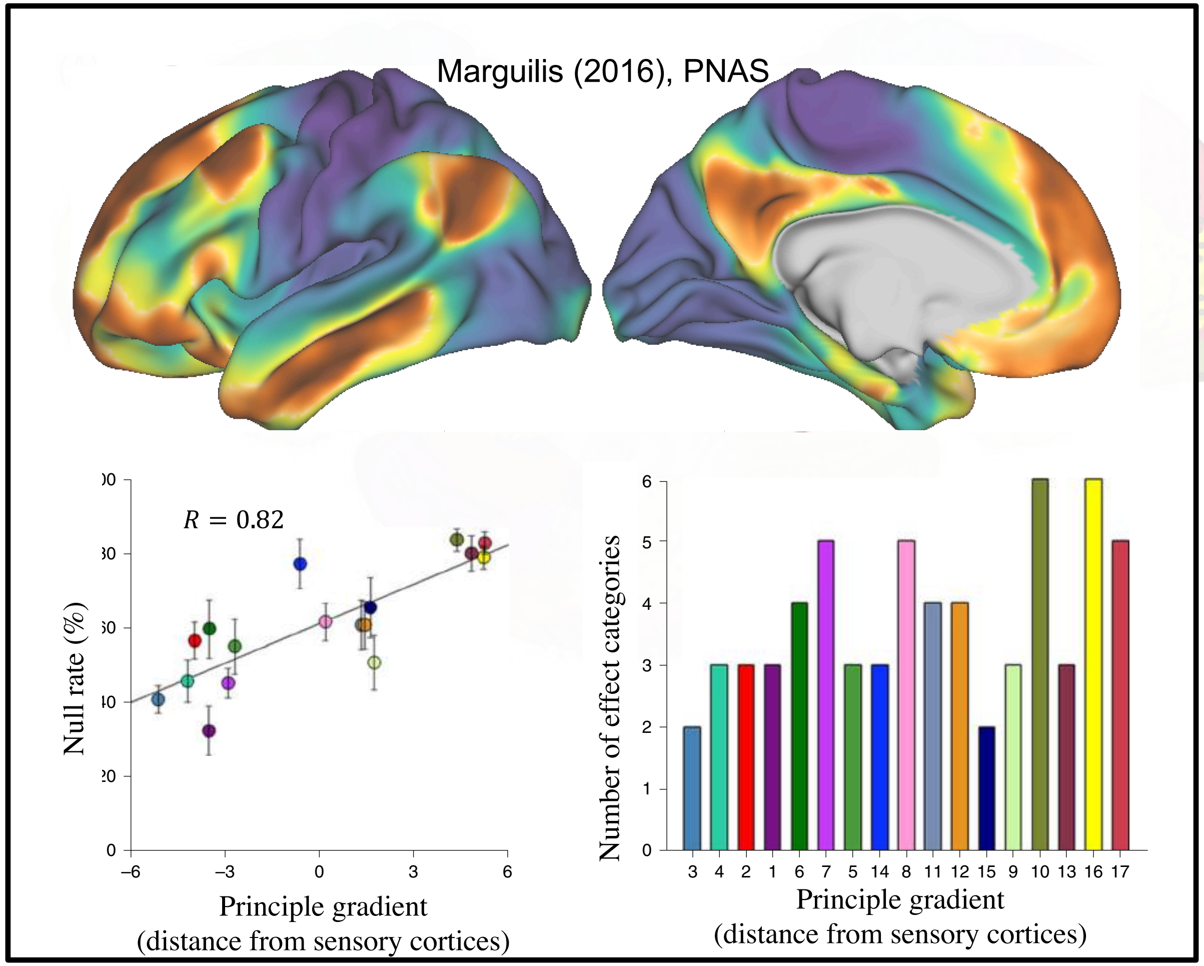
Parvizi et al. (2016) *JNeuro*

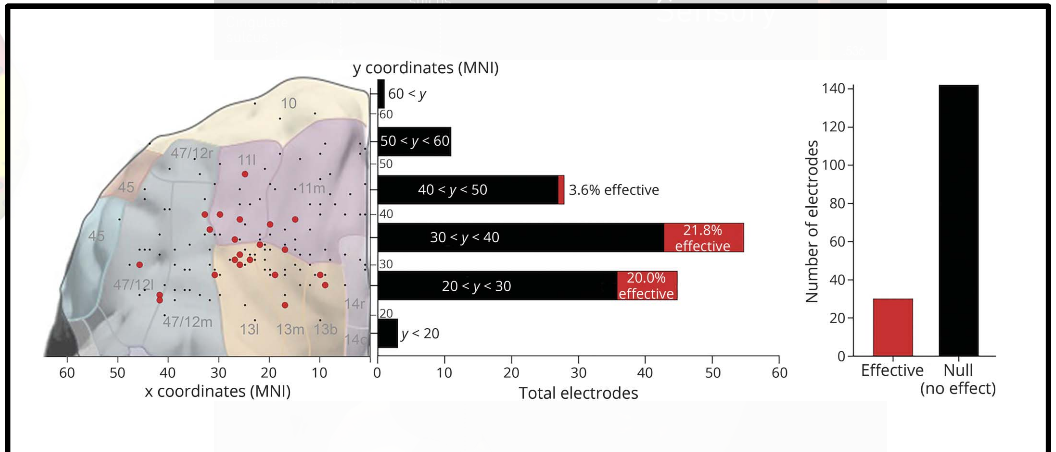


Fox et al. (2020), *Nature Human Behavior* (*News and Views* by C. Koch)

Elicitation rates across the cerebral cortex

Marguilis (2016), PNAS



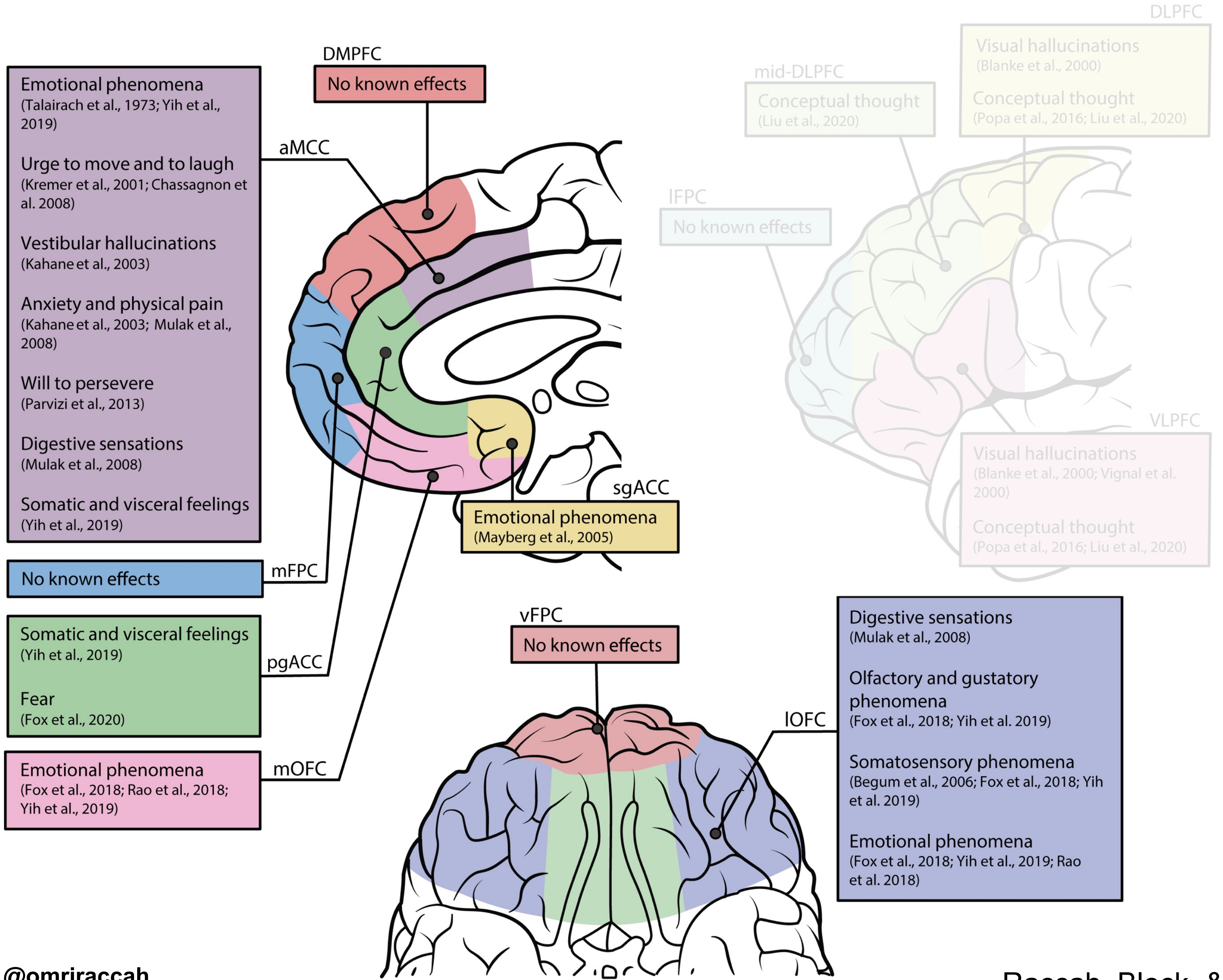


Fox*, Yih*, Raccah et al. (2018), *Neurology*

Trevisi et al. (2018), *Cortex*

Fox et al. (2020), *Nature Human Behavior* (*Views and News* by C. Koch)

iES to only certain PFC regions reliably alters experience



Raccah, Block, & Fox (2021) *JNeuro*

Conclusions and arguments

- There is no part of the brain wherein iES is *less* likely to cause a noticeable changes in consciousness than the most anterior portions of the PFC (Fox et al., 2020).

- Stimulation in only certain PFC regions – i.e., OFC and anterior ACC – reliably perturbs conscious experience.

- Effects in the OFC/ACC (e.g., visceral, olfactory, emotion) are devoid of visual and auditory experience across dozens of cases and display no clear relation to the immediate environment.

- Critically, the effects in OFC/ACC are consistent with their known functional roles supported by these regions (Bush et al, 2000; Devinsky et al. 1995; Rolls, 2004) – as are the few reliable effects of conceptual thought found in the lPFC (Berkovich-Ohana et al., 2020).

Hebb and Penfield, 1940; Mettler, 1949; Brickner, 1952; Pollen, 1999; Boly et al., 2017

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Stanford University

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Commentary by Naccache et al. (2021)

- The complex and distributed functional organization of the prefrontal cortex (PFC) – relative to sensory cortices – precludes its functional modulation by local intracranial electrical stimulation (iES).

Fox et al. (2020), *Nature Human Behavior* (*Views and News* by C. Koch)

Three empirical suggestions for moving the debate forward

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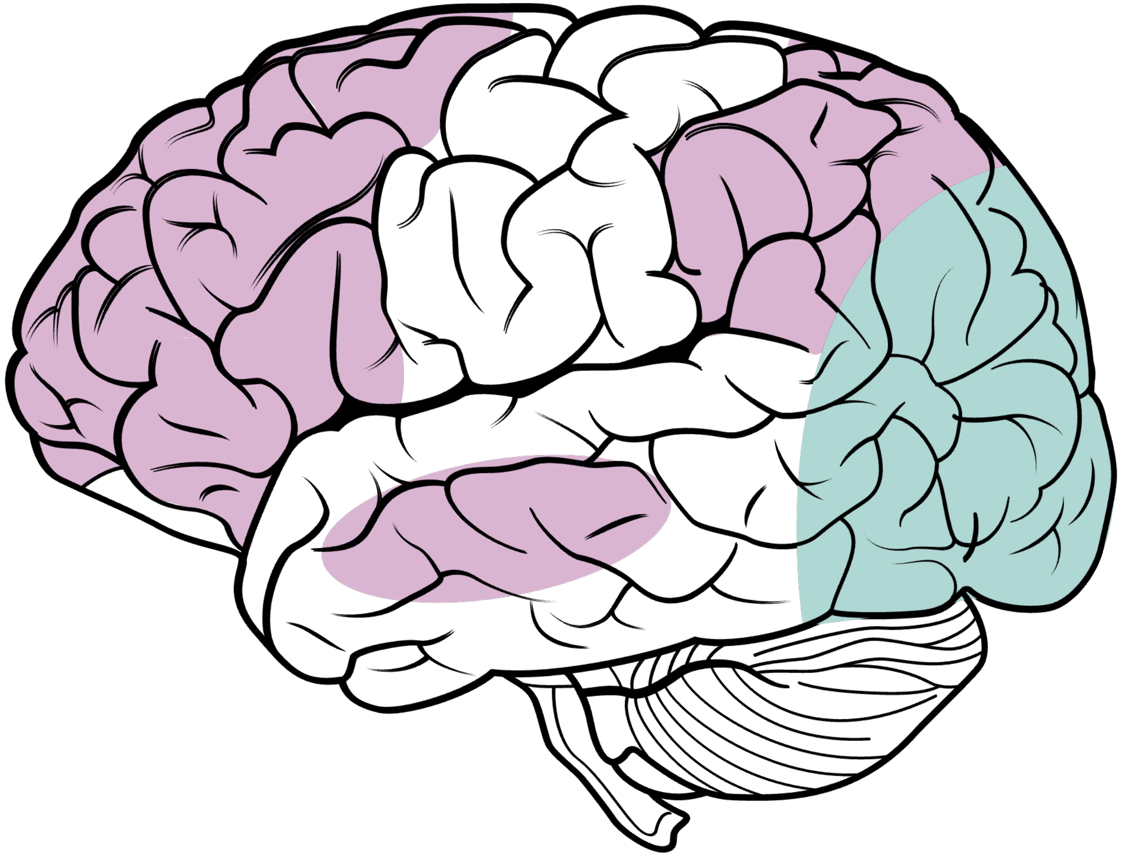
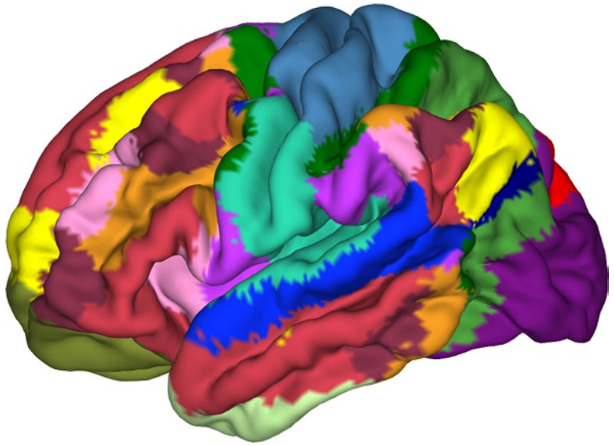
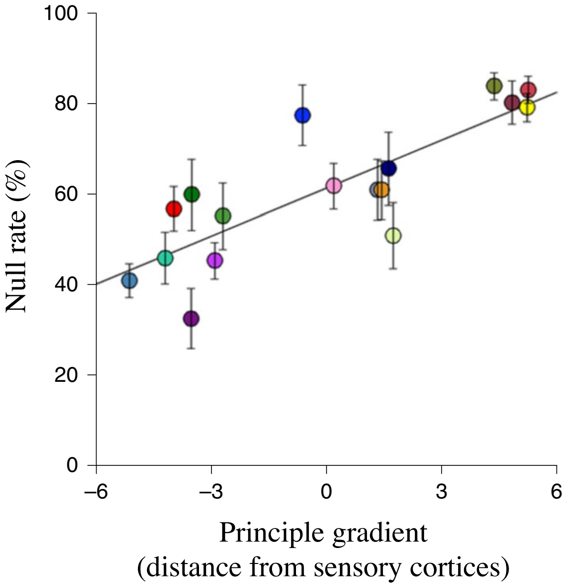


1. Clarifying null findings: *variance explained across the cerebral cortex*

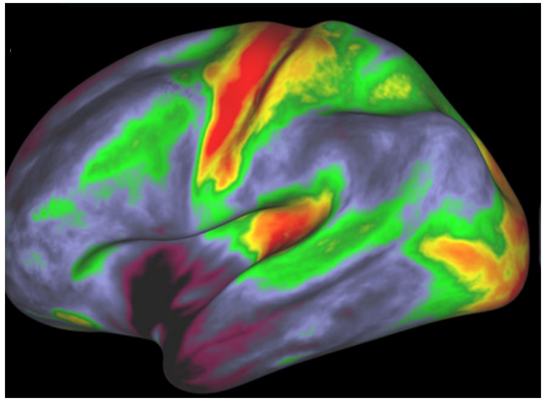
Yeo 17-network atlas

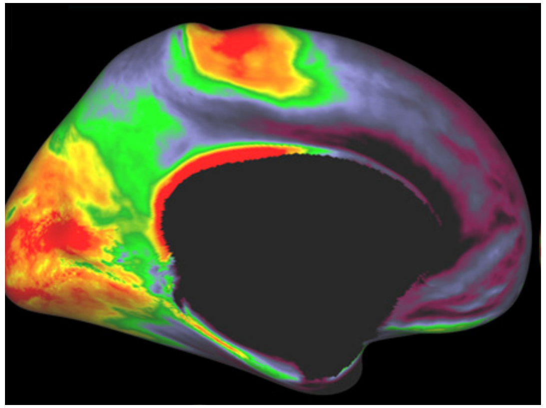




Elicitation rates cannot be explained by variations in either **tissue excitability** or **white matter density** (Fox et al., 2020)

$P = 0.784$

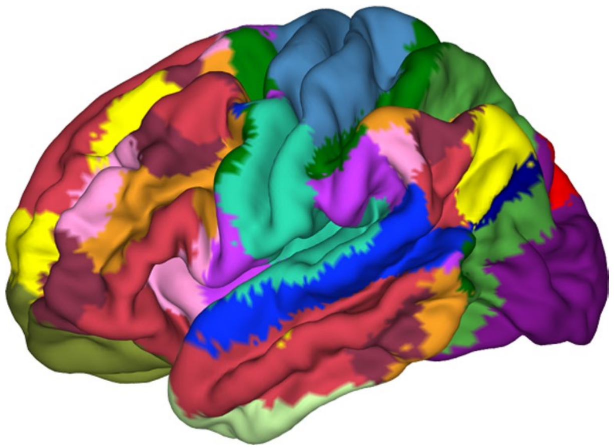


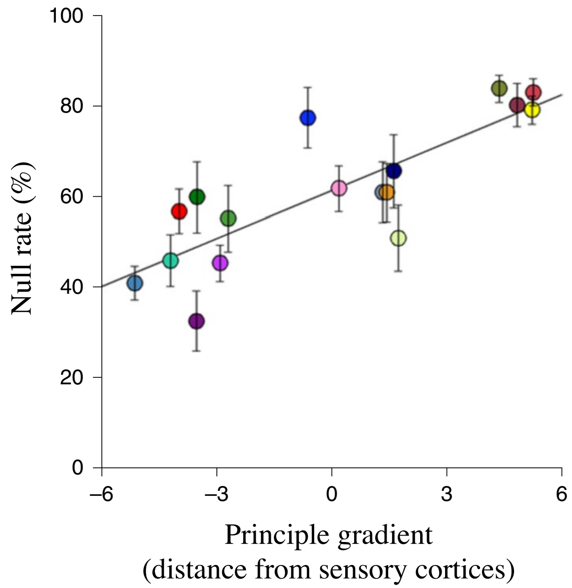


HCP; Glasser & Van Essen (2011)

Fox et al. (2020), *Nature Human Behavior*

1. Clarifying null findings: *variance explained across the cerebral cortex*





TRUE SCIENCE WAITS

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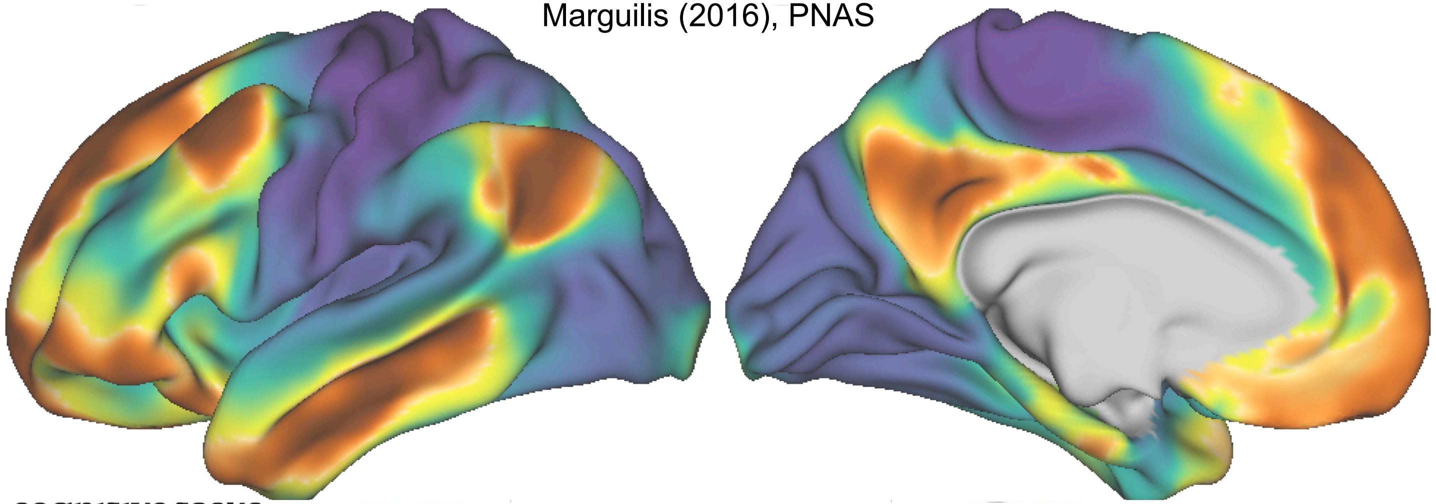
Marguilis (2016), PNAS



cognitive tasks

Mattia Rigotti, Omri Barak, Melissa R. Warden, Xiao-Jing Wang, Nathaniel D. Daw, Earl K. Miller & Stefano Fusi

Isolate measures of neuronal coding schemes across the cortex and compare these with iES null gradients

What the success of brain imaging implies about the neural code

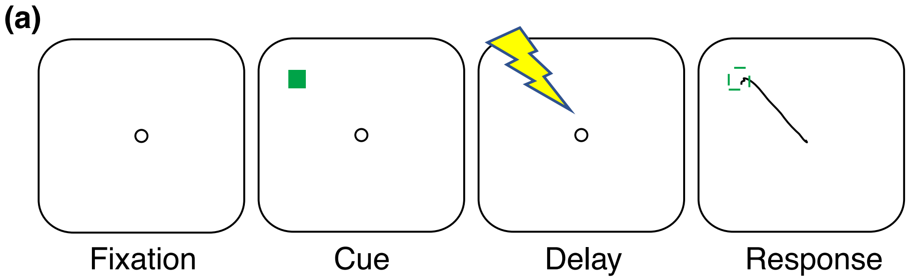
Olivia Guest, Bradley C Love
University College London, United Kingdom; The Alan Turing Institute, United Kingdom

Fox et al. (2020), *Nature Human Behavior*

2. Examining iES efficacy in PFC : closed-loop iES in controlled experiments

Working memory

Oculomotor delayed-response task

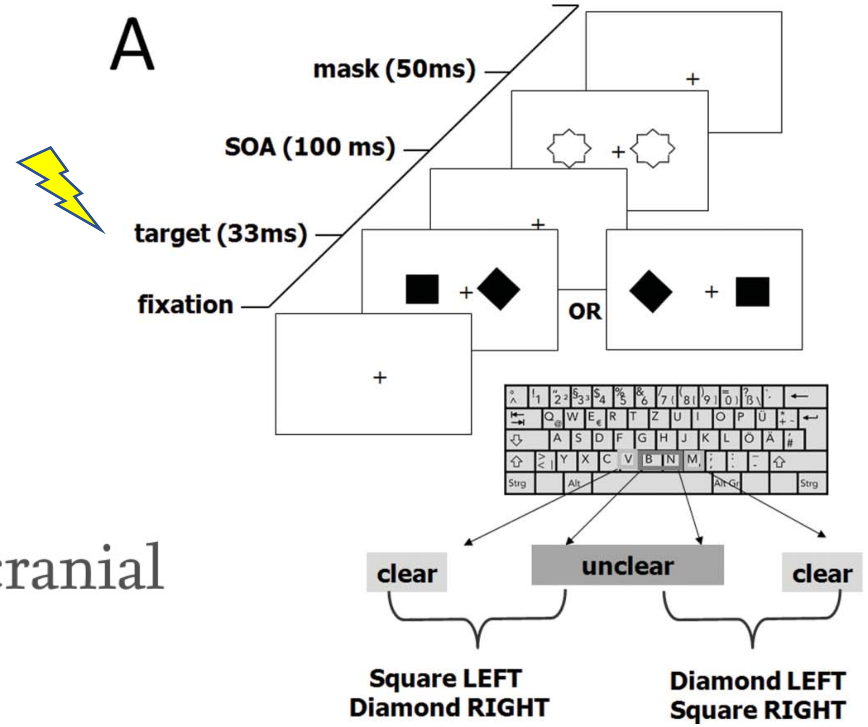


Curtis & D'Esposito (2003)

CLoSES: A platform for closed-loop intracranial stimulation in humans

Rina Zelmann [a], Angelique C. Paulk [a], Ishita Basu [b, c, k], Anish Sarma [d], Ali Yousefi [b, e], Britni Crocker [a, f], Emad Eskandar [c, g], Ziv Williams [c], G. Rees Cosgrove [h], Daniel S. Weisholtz [i], Darin D. Dougherty [b], Wilson Truccolo [d], Alik S. Widge [b, j], Sydney S. Cash [a]

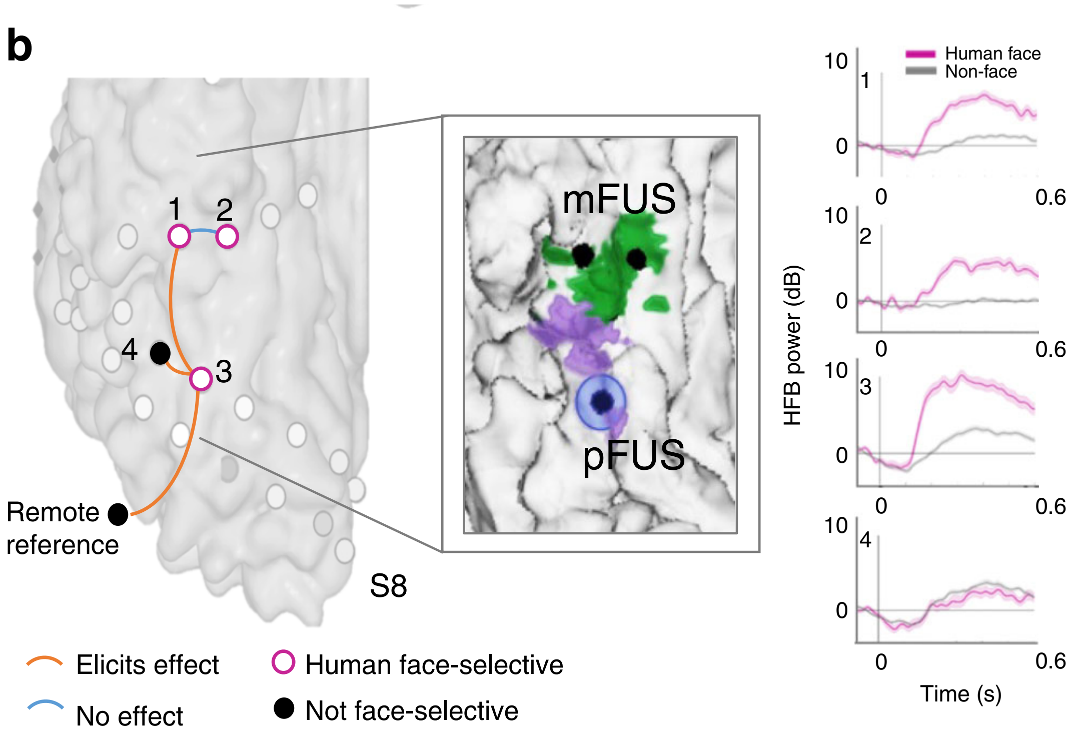
Metacognition



Rounis, Maniscalco et al. 2010

Del Cul, Dehaene et al. 2009
Fleming et al., 2014

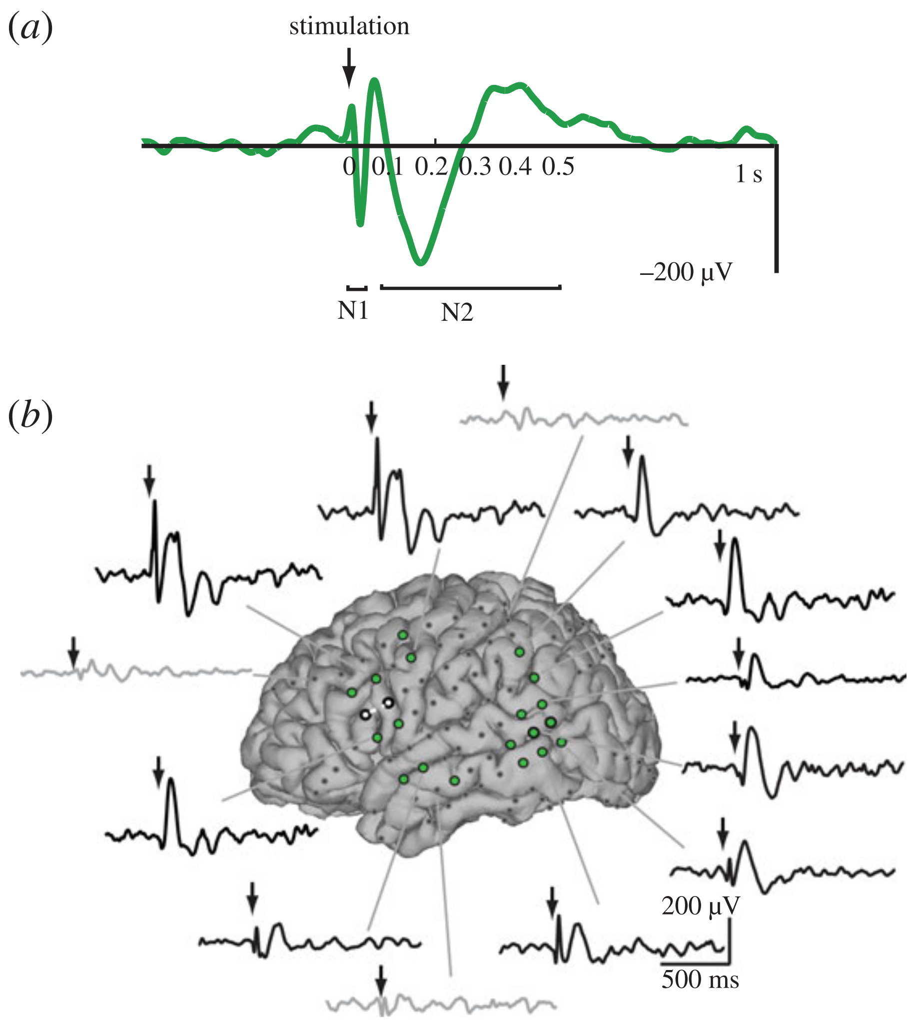
3. Clarifying findings outside the PFC: Whole-brain sampling methods



Schrouff, Raccah, et al. (2020), *Nature Comm*

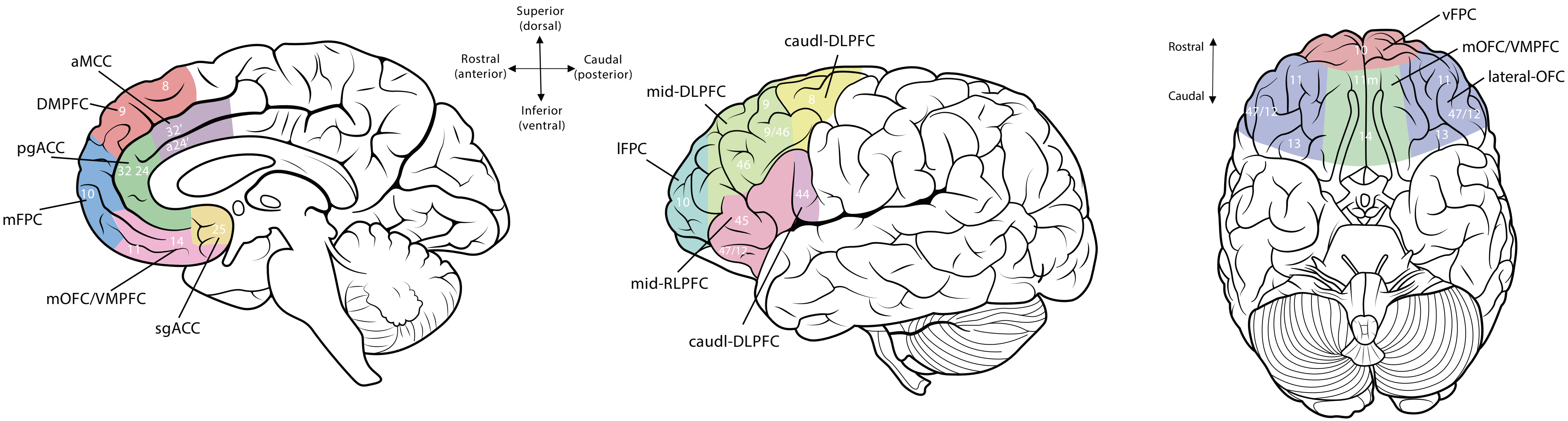
Does the spread of activity from sites that induce face distortion differ significantly in global AND local connectivity?

Corticocortical evoked potentials (CCEPs)



Keller et al. 2014

Anatomical parcellation of the human PFC



Raccah, Block, & Fox (2021) *JNeuro*

Fox et al. (2020): electrode distribution and excitability thresholds

Table 1 | Elicitation rates and current thresholds for the seven-network parcellation

Network	Electrodes			Current thresholds (mA)	
	Total	Responsive	Silent	Mean minimum elicitation threshold (±s.d.)	Mean maximum quiescence threshold (±s.d.)
Somatomotor	291	159 (54.6%)	132 (45.4%)	4.72 (1.80)	6.67 (2.15)
Visual	182	94 (51.7%)	88 (48.3%)	4.16 (2.16)	6.72 (1.45)
Dorsal attention	71	28 (39.4%)	43 (60.6%)	5.50 (2.38)	7.95 (2.24)
Salience	210	104 (49.5%)	106 (50.5%)	4.97 (1.76)	6.32 (1.92)
Frontoparietal	169	54 (32.0%)	115 (68.0%)	4.41 (1.89)	6.62 (1.99)
Limbic	195	47 (24.1%)	148 (75.9%)	4.41 (1.40)	5.82 (2.11)
Default	419	87 (20.8%)	332 (79.2%)	4.88 (2.09)	6.61 (2.02)
Totals and means	1,537	573 (37.3%)	964 (62.7%)	4.68 (1.94)	6.54 (2.04)

Fox et al. (2020): electrode distribution

Table 2 | Elicitation rates and current thresholds for the 17-network parcellation

Network	Electrodes			Current thresholds (mA)	
	Total	Responsive	Silent	Mean minimum elicitation threshold (±s.d.)	Mean maximum quiescence threshold (±s.d.)
01	52	35 (67.3%)	17 (32.7%)	4.21 (2.42)	6.44 (1.42)
02	102	44 (43.1%)	58 (56.9%)	3.83 (2.15)	6.61 (1.37)
03	175	103 (58.9%)	72 (41.1%)	4.39 (1.75)	6.31 (2.16)
04	78	42 (53.9%)	36 (46.1%)	5.34 (1.78)	7.22 (1.88)
05	47	21 (44.7%)	26 (55.3%)	5.05 (2.20)	8.41 (1.59)
06	40	16 (40.0%)	24 (60.0%)	5.69 (1.25)	7.17 (2.41)
07	156	85 (54.5%)	71 (45.5%)	5.07 (1.77)	6.34 (1.81)
08	97	37 (38.1%)	60 (61.9%)	4.61 (2.08)	6.11 (1.72)
09	49	24 (49.0%)	25 (51.0%)	4.25 (1.15)	6.00 (1.98)
10	149	24 (16.1%)	125 (83.9%)	4.81 (1.78)	5.71 (2.14)
11	54	21 (38.9%)	33 (61.1%)	4.86 (1.88)	6.54 (2.64)
12	59	23 (39.0%)	36 (61.0%)	4.14 (1.55)	7.06 (2.15)
13	71	14 (19.7%)	57 (80.3%)	5.69 (2.59)	6.63 (1.93)
14	40	9 (22.5%)	31 (77.5%)	6.11 (2.20)	7.96 (2.13)
15	35	12 (34.3%)	23 (65.7%)	4.38 (0.87)	6.76 (1.89)
16	173	36 (20.8%)	137 (79.2%)	4.38 (1.95)	6.37 (2.12)
17	160	27 (16.9%)	133 (83.1%)	4.88 (2.31)	6.78 (1.87)
Totals and means	1,537	573 (37.3%)	964 (62.7%)	4.68 (1.94)	6.54 (2.04)