

Chapter V Adventures into *terra incognita*: probing the neural circuits along the ventral visual stream

V.1. About neocortex

(Allman & McGuinness 1988, Allman 1999, Brodmann 1909, Finger 2000, Florio & Huttner 2014, Giannaris & Rosene 2012, Glickstein 1988, Herculano-Houzel 2009, Nieuwenhuys 1994, Rakic 1977, Rakic 2009, Sur & Leamey 2001, Van Essen 1997)

V.2. Connectivity to and from primary visual cortex

(Barone et al 2000, Binzegger et al 2004, Budd 1998, Callaway 1998a, Callaway 1998b, Callaway 2004, Cang et al 2005, Chapman et al 1996, Crowley & Katz 1999, Crowley & Katz 2000, Douglas et al 1995, Douglas & Martin 2004, Espinosa & Stryker 2012, Felleman & Van Essen 1991, Huberman 2007, Lund & Mustari 1977, Markov et al 2014, Miller 2016, Nassi & Callaway 2009, Rockland 2003, Rockland 2018, Rockland 2020, Rockland & Pandya 1979, Salin & Bullier 1995, Virga 1989, Wang & Burkhalter 2007, Wiesel & Hubel 1963)

V.3. The gold standard to study neural circuits

(Adrian 1926, Churchland & Sejnowski 1988, Kandel et al 2000, Koch 1999, Kreiman 2004, Sejnowski et al 1988)

V.4. Neurons in primary visual cortex respond selectively to bars shown at specific orientations

(De Valois et al 1982, Dumoulin & Wandell 2008, Hubel 1981, Hubel & Wiesel 1959, Hubel & Wiesel 1962, Hubel & Wiesel 1968, Hubel & Wiesel 1998, Livingstone 2013, Marg et al 1968, Spillmann 2014, Wiesel & Hubel 1974)

V.5. Complex neurons show tolerance to position changes

(De Valois et al 1982, Hubel 1963, Hubel 1979, Hubel 1981, Hubel & Wiesel 1962, Hubel & Wiesel 1968)

V.6. Nearby neurons show similar properties

(Horton & Hoyt 1991, Kaas 1997, Kremkow et al 2016, Maldonado et al 1997, Wiesel & Hubel 1974)

V.7. Quantitative phenomenological description of the responses in primary visual cortex

(Carandini & Heeger 1994, Carandini & Heeger 2011, Cavanaugh et al 2002, Dayan & Abbott 2001)

V.8. A simple model of orientation selectivity in primary visual cortex

(Anderson et al 2000, Carandini et al 2005, Hubel & Wiesel 1962, Hubel & Wiesel 1968, Kremkow et al 2016, Priebe & Ferster 2012, Serre et al 2007)

V.9. Many surprises left in V1

(Adesnik et al 2012, Adesnik 2010, Allman et al 1985, Angelucci & Bressloff 2006, Angelucci & Bullier 2003, Bair et al 2003, Benucci et al 2009, Carandini et al 2005, Gilbert et al 2009, Gomez-Laberge et al 2016, Hubener 2003, Keller et al 2012, Murphy et al 1999, Nassi et al 2014, Nassi et al 2013, Niell & Stryker 2010, Nurminen et al 2018, Olsen et al 2012, Olson & Pettigrew 1974, Piscopo et al 2013, Usrey & Reid 1999, Yao et al 2007, Zhou et al 2000, Zipser et al 1996)

V.10. Divide and conquer

(Anzai et al 2011, Born & Bradley 2005, Burkhalter & Van Essen 1986, Carlson et al 2011, Hegde & Van Essen 2000, Hegde & Van Essen 2006, Hubel & Wiesel 1959, Hubel & Wiesel 1968, Kusunoki et al 2006, Livingstone & Hubel 1988, Newsome et al 1989, Nowak et al 1999, Pasupathy & Connor 1999, Pasupathy & Connor 2001, Qiu & von der Heydt 2005)

V.11. We cannot exhaustively study all possible visual stimuli

(Bondar et al 2009, Kreiman 2019, McMahon et al 2014)

V.12. We live in the visual past: response latencies increase along the ventral stream

(Bair 1999, Butts et al 2007, Gawne & Martin 2000, Hung et al, 2005, Kohn 2007, Lamme et al 2002, Macknik 2007, Reich et al 2001a, Reich et al 2001b, Ringach et al 1997, Schmolesky et al 1998, Tovee 1994)

V.13. Receptive field sizes increase along the ventral visual stream

(Freeman & Simoncelli 2011, Kobatake & Tanaka 1994, Rolls 1991)

V.14. What do neurons beyond V1 prefer?

(Carandini et al 2005, Gallant et al 1993, Haxby et al 1991, Hegde & Van Essen 2003, Hegde & Van Essen 2007, Kobatake & Tanaka 1994, Kreiman 2004, Kreiman 2019, Pack et al 2006, Pasupathy & Connor 2001, Ramalingam et al

2013, Tolias et al 2001, Vangeneugden 2011, Vinje & Gallant 2000, Vinje & Gallant 2002, Womelsdorf et al 2007)

V.15. Brains construct their own interpretation of the world: the case of illusory contours

(Gawne & Martin 2000, Komatsu 2006, Lee 2003, Lee & Nguyen 2001, Leopold & Logothetis 1998, Martinez-Conde et al 2000, Peterhans & von der Heydt 1989, Peterhans & von der Heydt 1991, von der Heydt et al 1984)

V.16. A colorful V4

(Gegenfurtner 1997, Kusunoki et al 2006, Lennie & Movshon 2005, Livingstone & Hubel 1988, Motter 1994, Murphey et al 2008, Sacks 1997, Zeki 1983)

V.17. Attentional modulation

(Alitto & Usrey 2003, Baumann et al 1997, Bisley 2011, Chikkerur et al 2010, Crick 1984, Desimone & Duncan 1995, Ghose & Maunsell 2008, Gilbert & Li 2013, Lamme & Roelfsema 2000, Lee 2003, Lee & Nguyen 2001, Li et al 2004, Li 2014, Luck et al 1997, Markov et al 2014, Nassi et al 2014, Nassi et al 2013, Nurminen et al 2018, Posner & Gilbert 1999, Ramalingam et al 2013, Reynolds & Chelazzi 2004, Reynolds et al 1999, Reynolds & Heeger 2009, Roelfsema et al 2007, Saalmann et al 2007, Sing Lee et al 2002)

V.18. References

- Adesnik H, Bruns W, Taniguchi H, Huang ZJ, Scanziani M. 2012. A neural circuit for spatial summation in visual cortex. *Nature* 490: 226-31
- Adesnik H, Scanziani, M. 2010. Lateral competition for cortical space by layer-specific horizontal circuits. *Nature* 464: 1155-60
- Adrian E. 1926. The impulses produced by sensory nerve endings. Part 2: The response of a single end-organ. *Journal of Physiology* 61: 151-71
- Alitto HJ, Usrey WM. 2003. Corticothalamic feedback and sensory processing. *Current Opinion in Neurobiology* 13: 440-5
- Allman J, McGuinness E. 1988. Visual cortex in primates. *Comparative Primate Biology* 4: 279-326
- Allman J, Miezin F, McGuinness E. 1985. Stimulus specific responses from beyond the classical receptive field: neurophysiological mechanisms for local-global comparisons in visual neurons. *Annual Review of Neuroscience* 8: 407-30
- Allman JM. 1999. *Evolving brains*. New York: W.H. Freeman and Company.
- Anderson J, Carandini M, Ferster D. 2000. Orientation Tuning of Input Conductance, Excitation and Inhibition in Cat Primary Visual Cortex. *Journal of Neurophysiology* 84: 909-26

- Angelucci A, Bressloff PC. 2006. Contribution of feedforward, lateral and feedback connections to the classical receptive field center and extra-classical receptive field surround of primate V1 neurons. *Prog Brain Res* 154: 93-120
- Angelucci A, Bullier J. 2003. Reaching beyond the classical receptive field of V1 neurons: horizontal or feedback axons? *J Physiol Paris* 97: 141-54
- Anzai A, Chowdhury S, DeAngelis G. 2011. Coding of Stereoscopic Depth Information in Visual Areas V3 and V3A. *The Journal of Neuroscience* 31: 10270-82
- Bair W. 1999. Spike timing in the mammalian visual system. *Current Opinion in Neurobiology* 9: 447-53
- Bair W, Cavanaugh JR, Movshon JA. 2003. Time course and time-distance relationships for surround suppression in macaque V1 neurons. *Journal of Neuroscience* 23: 7690-701
- Barone P, Batardiere A, Knoblauch K, Kennedy H. 2000. Laminar distribution of neurons in extrastriate areas projecting to visual areas V1 and V4 correlates with the hierarchical rank and indicates the operation of a distance rule. *Journal of Neuroscience* 20: 3263-81
- Baumann R, van der Zwan R, Peterhans E. 1997. Figure-ground segregation at contours: a neural mechanism in the visual cortex of the alert monkey. *Eur. J. Neurosci.* 9: 1290-303
- Benucci A, Ringach DL, Carandini M. 2009. Coding of stimulus sequences by population responses in visual cortex. *Nature Neuroscience* 12: 1317-24
- Binzegger T, Douglas RJ, Martin KA. 2004. A quantitative map of the circuit of cat primary visual cortex. *Journal of Neuroscience* 24: 8441-53
- Bisley J. 2011. The neural basis of visual attention. *The Journal of physiology* 589: 49-57
- Bondar I, Leopold D, Richmond B, Victor J, Logothetis N. 2009. Long-term stability of visual pattern selective responses of monkey temporal lobe neurons *PloS One* 9
- Born RT, Bradley DC. 2005. Structure and function of visual area MT. *Annu Rev Neurosci* 28: 157-89
- Brodmann K. 1909. *Vergleichende Lokalisationslehre der Grosshirnrinde in ihren Prinzipien dargestellt auf Grund des Zellenbaues*. Leipzig: Barth.
- Budd J. 1998. Extrastriate feedback to primary visual cortex in primates: a quantitative analysis of connectivity. *The Royal Society* 265: 1037-44
- Burkhalter A, Van Essen DC. 1986. Processing of color, form and disparity information in visual areas VP and V2 of ventral extrastriate cortex in the macaque monkey. *Journal of Neuroscience* 6: 2327-51
- Butts DA, Weng C, Jin J, Yeh CI, Lesica NA, et al. 2007. Temporal precision in the neural code and the timescales of natural vision. *Nature* 449: 92-5
- Callaway EM. 1998a. Local circuits in primary visual cortex of the macaque monkey. *Annu Rev Neurosci* 21: 47-74
- Callaway EM. 1998b. Prenatal development of layer-specific local circuits in primary visual cortex of the macaque monkey. *Journal of Neuroscience* 18: 1505-27
- Callaway EM. 2004. Feedforward, feedback and inhibitory connections in primate visual cortex. *Neural Netw* 17: 625-32

- Cang J, Renteria RC, Kaneko M, Liu X, Copenhagen DR, Stryker MP. 2005. Development of precise maps in visual cortex requires patterned spontaneous activity in the retina. *Neuron* 48: 797-809
- Carandini M, Demb JB, Mante V, Tolhurst DJ, Dan Y, et al. 2005. Do we know what the early visual system does? *Journal of Neuroscience* 25: 10577-97
- Carandini M, Heeger DJ. 1994. Summation and division by neurons in primate visual cortex. *Science* 264: 1333-6
- Carandini M, Heeger DJ. 2011. Normalization as a canonical neural computation. *Nature Reviews Neuroscience* 13: 51-62
- Carlson ET, Rasquinha RJ, Zhang K, Connor CE. 2011. A sparse object coding scheme in area V4. *Current Biology* 21: 288-93
- Cavanaugh JR, Bair W, Movshon JA. 2002. Nature and interaction of signals from the receptive field center and surround in macaque V1 neurons. *J Neurophysiol* 88: 2530-46
- Chapman B, Stryker M, Bonhoeffer T. 1996. Development of Orientation Preference Maps in Ferret Primary Visual Cortex. *Journal of Neuroscience* 16: 6443-53
- Chikkerur S, Serre T, Tan C, Poggio T. 2010. What and where: A bayesian inference theory of attention. *Vision research* 50: 2233-47
- Churchland PS, Sejnowski TJ. 1988. Perspectives on Cognitive Neuroscience. *Science* 242: 741-45
- Crick F. 1984. Function of the thalamic reticular complex: the searchlight hypothesis. *PNAS* 81: 4586-90
- Crowley JC, Katz LC. 1999. Development of ocular dominance columns in the absence of retinal input. *Nature Neuroscience* 2: 1125-30
- Crowley JC, Katz LC. 2000. Early development of ocular dominance columns. *Science* 290: 1321-4
- Dayan P, Abbott L. 2001. *Theoretical Neuroscience*. Cambridge: MIT Press.
- De Valois RL, Albrecht DG, Thorell LG. 1982. Spatial frequency selectivity of cells in macaque visual cortex. *Vision research* 22: 545-59
- Desimone R, Duncan J. 1995. Neural mechanisms of selective visual attention. *Annual Review of Neuroscience* 18: 193-222
- Douglas RJ, Koch C, Mahowald M, Martin KA, Suarez HH. 1995. Recurrent excitation in neocortical circuits. *Science* 269: 981-5
- Douglas RJ, Martin KA. 2004. Neuronal circuits of the neocortex. *Annu Rev Neurosci* 27: 419-51
- Dumoulin SO, Wandell BA. 2008. Population receptive field estimates in human visual cortex. *Neuroimage* 39: 647-60
- Espinosa JS, Stryker MP. 2012. Development and plasticity of the primary visual cortex. *Neuron* 75: 230-49
- Felleman DJ, Van Essen DC. 1991. Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex* 1: 1-47
- Finger S. 2000. *Minds behind the brain. A history of the pioneers and their discoveries*. New York: Oxford University Press.
- Florio M, Huttner WB. 2014. Neural progenitors, neurogenesis and the evolution of the neocortex. *Development* 141: 2182-94

- Freeman J, Simoncelli EP. 2011. Metamers of the ventral stream. *Nature Neuroscience* 14: 1195-201
- Gallant JL, Braun J, Van Essen DC. 1993. Selectivity for polar, hyperbolic, and Cartesian gratings in macaque visual cortex. *Science* 259: 100-3
- Gawne T, Martin J. 2000. Activity of primate V1 cortical neurons during blinks. *Journal of Neurophysiology* 84: 2691-94
- Gegenfurtner KR. 1997. Visual neurobiology: colouring the cortex. *Nature* 388: 23-24
- Ghose GM, Maunsell JH. 2008. Spatial summation can explain the attentional modulation of neuronal responses to multiple stimuli in area V4. *Journal of Neuroscience* 28: 5115-26
- Giannaris EL, Rosene DL. 2012. A stereological study of the numbers of neurons and glia in the primary visual cortex across the lifespan of male and female rhesus monkeys. *J Comp Neurol* 520: 3492-508
- Gilbert CD, Li W. 2013. Top-down influences on visual processing. *Nat Rev Neurosci* 14: 350-63
- Gilbert CD, Li W, Piech V. 2009. Perceptual learning and adult cortical plasticity. *The Journal of physiology* 587: 2743-51
- Glickstein M. 1988. The discovery of the visual cortex. *Scientific American* Sept.: 84-91
- Gomez-Laberge C, Smolyanskaya A, Nassi JJ, Kreiman G, Born R. 2016. Bottom-Up and Top-Down Input Augment the Variability of Cortical Neurons. *Neuron* 91: 540-47
- Haxby J, Grady C, Horwitz B, Ungerleider L, Mishkin M, et al. 1991. Dissociation of object and spatial visual processing pathways in human extrastriate cortex. *PNAS* 88: 1621-25
- Hegde J, Van Essen D. 2000. Selectivity for Complex Shapes in Primate Visual Area V2. *The Journal of Neuroscience* 20: 6
- Hegde J, Van Essen D. 2006. Temporal dynamics of 2D and 3D shape representation in macaque visual area V4. *Visual Neuroscience* 23: 14
- Hegde J, Van Essen DC. 2003. Strategies of shape representation in macaque visual area V2. *Vis Neurosci* 20: 313-28
- Hegde J, Van Essen DC. 2007. A comparative study of shape representation in macaque visual areas v2 and v4. *Cerebral Cortex* 17: 1100-16
- Herculano-Houzel S. 2009. The human brain in numbers: a linearly scaled-up primate brain. *Frontiers in Human Neuroscience* 3
- Horton JC, Hoyt WF. 1991. The representation of the visual field in human striate cortex. *Archives in Ophtalmology* 109: 816-24
- Hubel D. 1963. The Visual Cortex of the Brain: A start toward understanding how it analyzes images on the retina can be made through studies of the responses that individual cells in the visual system of the cat give to varying patterns of light. *Scientific American*: 54-63
- Hubel D. 1979. The Brain. *Scientific American* 241: 45-53
- Hubel D. 1981. Evolution of ideas on the primary visual cortex, 1955-1978: a biased historical account. In *Nobel Lectures*

- Hubel D, Wiesel T. 1959. Receptive fields of single neurons in the cat's striate cortex. *Journal of Physiology (London)* 148: 574-91
- Hubel DH, Wiesel TN. 1962. Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *The Journal of physiology* 160: 106-54
- Hubel DH, Wiesel TN. 1968. Receptive fields and functional architecture of monkey striate cortex. *The Journal of physiology* 195: 215-43
- Hubel DH, Wiesel TN. 1998. Early exploration of the visual cortex. *Neuron* 20: 401-12.
- Hubener M. 2003. Mouse visual cortex. *Current Opinion in Neurobiology* 13: 413-20
- Huberman AD. 2007. Mechanisms of eye-specific visual circuit development. *Current Opinion in Neurobiology* 17: 73-80
- Hung CP, Kreiman G, Poggio T, DiCarlo JJ. 2005. Fast Read-out of Object Identity from Macaque Inferior Temporal Cortex. *Science* 310: 863-66
- Kaas J. 1997. Topographic maps are fundamental to sensory processing. *Brain Research Bulletin* 44: 107-12
- Kandel E, Schwartz J, Jessell T. 2000. *Principles of Neural Science*. New York: McGraw-Hill.
- Keller G, Bonhoeffer T, Hubener M. 2012. Sensorimotor Mismatch Signals in Primary Visual Cortex of the Behaving Mouse. *Neuron* 74: 809-16
- Kobatake E, Tanaka K. 1994. Neuronal selectivities to complex object features in the ventral visual pathway of the macaque cerebral cortex. *J Neurophysiol* 71: 856-67
- Koch C. 1999. *Biophysics of Computation*. New York: Oxford University Press.
- Kohn A. 2007. Visual adaptation: physiology, mechanisms, and functional benefits. *J Neurophysiol* 97: 3155-64
- Komatsu H. 2006. The neural mechanisms of perceptual filling-in. *Nat Rev Neurosci* 7: 220-31
- Kreiman G. 2004. Neural coding: computational and biophysical perspectives. *Physics of Life Reviews* 2: 71-102
- Kreiman G. 2019. What do neurons really want? The role of semantics in cortical representations In *Psychology of Learning and Motivation*, ed. D Beck
- Kremkow J, Jin J, Wang Y, Alonso JM. 2016. Principles underlying sensory map topography in primary visual cortex. *Nature* 533: 52-7
- Kusunoki M, Moutoussis K, Zeki S. 2006. Effect of background colors on the tuning of color-selective cells in monkey area V4. *J Neurophysiol* 95: 3047-59
- Lamme VA, Roelfsema PR. 2000. The distinct modes of vision offered by feedforward and recurrent processing. *Trends Neurosci* 23: 571-9
- Lamme VA, Zipser K, Spekreijse H. 2002. Masking interrupts figure-ground signals in V1. *J Cogn Neurosci* 14: 1044-53
- Lee TS. 2003. Computations in the early visual cortex. *J Physiol Paris* 97: 121-39
- Lee TS, Nguyen M. 2001. Dynamics of subjective contour formation in the early visual cortex. *Proceedings of the National Academy of Sciences of the United States of America* 98: 1907-11
- Lennie P, Movshon JA. 2005. Coding of color and form in the geniculostriate visual pathway. *J Opt Soc Am A Opt Image Sci Vis* 22: 2013-33

- Leopold D, Logothetis N. 1998. Microsaccades differentially modulate neural activity in the striate and extrastriate visual cortex. *Experimental Brain Research* 123: 341-45
- Li W, Piech V, Gilbert CD. 2004. Perceptual learning and top-down influences in primary visual cortex. *Nature Neuroscience* 7: 651-7
- Li Z. 2014. *Understanding Vision*. Oxford University Press.
- Livingstone M. 2013. David Hubel: In Memoriam. *Neuron*
- Livingstone M, Hubel D. 1988. Segregation of form, color, movement and depth: anatomy, physiology and perception. *Science* 240: 740-49
- Luck SJ, Chelazzi L, Hillyard SA, Desimone R. 1997. Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. *J Neurophysiol* 77: 24-42
- Lund R, Mustari M. 1977. Development of the geniculocortical pathway in rat. *J Comp Neurol* 173: 289-305
- Macknik SL, Martinez-Conde, S. 2007. The role of feedback in visual masking and visual processing. *Advances in Cognitive Psychology* 3: 125-53
- Maldonado PE, Godecke I, Gray CM, Bonhoeffer T. 1997. Orientation selectivity in pinwheel centers in cat striate cortex. *Science* 276: 1551-55
- Marg E, Adams JE, Rutkin B. 1968. Receptive fields of cells in the human visual cortex. *Experientia* 24: 348-50
- Markov NT, Ercsey-Ravasz MM, Ribeiro Gomes AR, Lamy C, Magrou L, et al. 2014. A Weighted and Directed Interareal Connectivity Matrix for Macaque Cerebral Cortex. *Cerebral Cortex* 24: 17-36
- Martinez-Conde S, Macknik SL, Hubel DH. 2000. Microsaccadic eye movements and firing of single cells in the striate cortex of macaque monkeys. *Nature Neuroscience* 3: 251-58
- McMahon DB, Jones AP, Bondar IV, Leopold DA. 2014. Face-selective neurons maintain consistent visual responses across months. *Proceedings of the National Academy of Sciences of the United States of America* 111: 8251-6
- Miller KD. 2016. Canonical computations of cerebral cortex. *Current Opinion in Neurobiology* 37: 75-84
- Motter BC. 1994. Neural correlates of attentive selection for color or luminance in extrastriate area V4. *Journal of Neuroscience* 14: 2178-89
- Murphey DK, Yoshor D, Beauchamp MS. 2008. Perception matches selectivity in the human anterior color center. *Current Biology* 18: 216-20
- Murphy P, Duckett S, Sillito A. 1999. Feedback connections to the lateral geniculate nucleus and cortical response properties. *Science* 286: 1552-54
- Nassi J, Gomez-Laberge C, Kreiman G, Born R. 2014. Corticocortical feedback increases the spatial extent of normalization. *Frontiers in Systems Neuroscience* 8
- Nassi J, Lomber S, Born R. 2013. Corticocortical Feedback Contributes to Surround Suppression in V1 of the Alert Primate. *Journal of Neuroscience* 33: 8504
- Nassi JJ, Callaway EM. 2009. Parallel processing strategies of the primate visual system. *Nat Rev Neurosci* 10: 360-72
- Newsome W, Britten K, Movshon J. 1989. Neuronal correlates of a perceptual decision. *Nature* 341: 52-54

- Niell CM, Stryker MP. 2010. Modulation of visual responses by behavioral state in mouse visual cortex. *Neuron* 65: 472-9
- Nieuwenhuys R. 1994. The neocortex. An overview of its evolutionary development, structural organization and synaptology. *Anat Embryol (Berl)* 190: 307-37
- Nowak LG, Munk MHJ, James AC, Girard P, Bullier J. 1999. Cross-Correlation Study of the Temporal Interactions Between Areas V1 and V2 of the Macaque Monkey. *The American Physiology Society*: 17
- Nurminen L, Merlin S, Bijanzadeh M, Federer F, Angelucci A. 2018. Top-down feedback controls spatial summation and response amplitude in primate visual cortex. *Nature Communications* 9: 2281
- Olsen SR, Bortone DS, Adesnik H, Scanziani M. 2012. Gain control by layer six in cortical circuits of vision. *Nature* 483: 5
- Olson CR, Pettigrew JD. 1974. Single units in visual cortex of kittens reared in stroboscopic illumination. *Brain Res* 70: 189-204
- Pack CC, Conway BR, Born RT, Livingstone MS. 2006. Spatiotemporal structure of nonlinear subunits in macaque visual cortex. *J. Neurosci.* 26: 893-907
- Pasupathy A, Connor C. 1999. Responses to contour features in macaque area V4. *Journal of Neurophysiology* 82: 2490-502
- Pasupathy A, Connor CE. 2001. Shape representation in area V4: position-specific tuning for boundary conformation. *J Neurophysiol* 86: 2505-19
- Peterhans E, von der Heydt R. 1989. Mechanisms of contour perception in monkey visual cortex. II. Contours bridging gaps. *J. Neurosci.* 9: 1749-63
- Peterhans E, von der Heydt R. 1991. Subjective contours - bridging the gap between psychophysics and physiology. *Trends in Neuroscience* 14: 112-19
- Piscopo DM, El-Danaf RN, Huberman AD, Niell CM. 2013. Diverse visual features encoded in mouse lateral geniculate nucleus. *Journal of Neuroscience* 33: 4642-56
- Posner MI, Gilbert CD. 1999. Attention and primary visual cortex. *Proceedings of the National Academy of Sciences of the United States of America* 96: 2585-7
- Priebe NJ, Ferster D. 2012. Mechanisms of neuronal computation in mammalian visual cortex. *Neuron* 75: 194-208
- Qiu FT, von der Heydt R. 2005. Figure and ground in the visual cortex: v2 combines stereoscopic cues with gestalt rules. *Neuron* 47: 155-66
- Rakic P. 1977. Prenatal development of the visual system in rhesus monkey. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* 278: 245-60
- Rakic P. 2009. Evolution of the neocortex: a perspective from developmental biology. *Nat Rev Neurosci* 10: 724-35
- Ramalingam N, McManus JN, Li W, Gilbert CD. 2013. Top-down modulation of lateral interactions in visual cortex. *Journal of Neuroscience* 33: 1773-89
- Reich D, Mechler F, Victor J. 2001a. Independent and redundant information in nearby cortical neurons. *Science* 294: 2566-68
- Reich DS, Mechler F, Victor JD. 2001b. Temporal coding of contrast in primary visual cortex: when, what, and why. *J Neurophysiol* 85: 1039-50
- Reynolds JH, Chelazzi L. 2004. Attentional modulation of visual processing. *Annu Rev Neurosci* 27: 611-47

- Reynolds JH, Chelazzi L, Desimone R. 1999. Competitive mechanisms subserve attention in macaque areas V2 and V4. *Journal of Neuroscience* 19: 1736-53
- Reynolds JH, Heeger DJ. 2009. The normalization model of attention. *Neuron* 61: 168
- Ringach DL, Hawken MJ, Shapley R. 1997. Dynamics of orientation tuning in macaque primary visual cortex. *Nature* 387: 281-4
- Rockland K. 2003. Feedback Connections: Splitting the Arrow. *The primate visual system*
- Rockland KS. 2018. Axon Collaterals and Brain States. *Front Syst Neurosci* 12: 32
- Rockland KS. 2020. What we can learn from the complex architecture of single axons. *Brain Struct Funct* 225: 1327-47
- Rockland KS, Pandya DN. 1979. Laminar origins and terminations of cortical connections of the occipital lobe in the rhesus monkey. *Brain Res* 179: 3-20
- Roelfsema PR, Tolboom M, Khayat PS. 2007. Different processing phases for features, figures, and selective attention in the primary visual cortex. *Neuron* 56: 785-92
- Rolls E. 1991. Neural organization of higher visual functions. *Current Opinion in Neurobiology* 1: 274-78
- Saalman YB, Pigarev IN, Vidyasagar TR. 2007. Neural mechanisms of visual attention: how top-down feedback highlights relevant locations. *Science* 316: 1612-5
- Sacks O. 1997. *The Island of the Colorblind*. New York: Alfred A. Knopf, Inc.
- Salin PA, Bullier J. 1995. Corticocortical connections in the visual system: structure and function. *Physiol Rev* 75: 107-54
- Schmolesky M, Wang Y, Hanes D, Thompson K, Leutgeb S, et al. 1998. Signal timing across the macaque visual system. *Journal of Neurophysiology* 79: 3272-78
- Sejnowski T, Koch C, Churchland P. 1988. Computational neuroscience. *Science* 241: 1299-306
- Serre T, Kreiman G, Kouh M, Cadieu C, Knoblich U, Poggio T. 2007. A quantitative theory of immediate visual recognition. *Progress In Brain Research* 165C: 33-56
- Sing Lee T, Yang CF, Romero RD, Mumford D. 2002. Neural activity in early visual cortex reflects behavioral experience and higher-order perceptual saliency. *Nature Neuroscience* 5: 589-97
- Spillmann L. 2014. Receptive fields of visual neurons: the early years. *Perception* 43: 1145-76
- Sur M, Leamey CA. 2001. Development and plasticity of cortical areas and networks. *Nat Rev Neurosci* 2: 251-62
- Tolias AS, Moore T, Smirnakis SM, Tehovnik EJ, Siapas AG, Schiller PH. 2001. Eye movements modulate visual receptive fields of V4 neurons. *Neuron* 29: 757-67
- Tovee MJ. 1994. Neuronal processing. How fast is the speed of thought? *Current Biology* 4: 1125-7
- Usrey WM, Reid RC. 1999. Synchronous activity in the visual system. *Annual Review of Physiology* 61: 435-56
- Van Essen DC. 1997. A tension-based theory of morphogenesis and compact wiring in the central nervous system. *Nature* 385: 313-18

- Vangeneugden J, De Maziere, PA, Van Hulle, MM, Jaeggli, T., Van Gool, L., Vogels, R. 2011. Distinct Mechanisms for Coding of Visual Actions in Macaque Temporal Cortex. *The Journal of Neuroscience* 31: 385-401
- Vinje WE, Gallant JL. 2000. Sparse coding and decorrelation in primary visual cortex during natural vision. *Science* 287: 1273-6
- Vinje WE, Gallant JL. 2002. Natural stimulation of the nonclassical receptive field increases information transmission efficiency in V1. *Journal of Neuroscience* 22: 2904-15
- Virga A, Rockland, KS. 1989. Terminal Arbors of Individual "Feedback" Axons Projecting from Area V2 to V1 in the Macaque Monkey: A Study Using Immunohistochemistry of Anterogradely Transported Phaseolus vulgaris-leucoagglutinin. *The Journal of Comparative Neurology* 285: 54-72
- von der Heydt R, Peterhans E, Baumgartner G. 1984. Illusory contours and cortical neuron responses. *Science* 224: 1260-62
- Wang Q, Burkhalter A. 2007. Area map of mouse visual cortex. *J Comp Neurol* 502: 339-57
- Wiesel TN, Hubel DH. 1963. Single-Cell Responses in Striate Cortex of Kittens Deprived of Vision in One Eye. *J Neurophysiol* 26: 1003-17
- Wiesel TN, Hubel DH. 1974. Ordered arrangement of orientation columns in monkeys lacking visual experience. *J Comp Neurol* 158: 307-18
- Womelsdorf T, Schoffelen JM, Oostenveld R, Singer W, Desimone R, et al. 2007. Modulation of neuronal interactions through neuronal synchronization. *Science* 316: 1609-12
- Yao H, Shi L, Han F, Gao H, Dan Y. 2007. Rapid learning in cortical coding of visual scenes. *Nature Neuroscience* 10: 772-8
- Zeki S. 1983. Color coding in the cerebral cortex - The reaction of cells in monkey visual cortex to wavelengths and colors. *Neuroscience* 9: 741-65
- Zhou H, Friedman HS, von der Heydt R. 2000. Coding of border ownership in monkey visual cortex. *J. Neurosci.* 20: 6594-611
- Zipser K, Lamme VA, Schiller PH. 1996. Contextual modulation in primary visual cortex. *Journal of neuroscience* 16: 7376-89