Lecture 3: Hierarchical Organisation of Primate visual System

laminar connections and hierarchical rank for areas above V1 $^{\left[1 ight]}$

- ascending connections arise in supragranular layers & terminate in layer 4;
- feedback connections arise in infragranular layers & terminate in layers 1 & 6;

NB. these observations apply more strictly to connections that traverse more than one tier in the hierarchy;

- lateral connections have an intermediate pattern; plus
- rule 2: reciprocity: a forward pattern is always reciprocated by a feedback pattern (or vice versa);
- rule 3: transitivity: if A to B is 'forward' and B to C is 'forward', then A to C will be 'forward';
- rules permit construction of a systematic hierarchy, with multiple, precisely defined ranks.

The ventral visual pathway for object recognition

- Can be identified by the physiological properties of serial areas; not necessarily a discrete 'pathway' in anatomical terms;

Greater sophistication of response properties at higher levels, e.g.

- Hubel & Wiesel's classification/hypothesis of simple, complex & hypercomplex RFs in (cat) areas 17, 18 19;
- areas V2 & V4 and response to illusory (or 'anomalous') contours; [2 3]
- area V4 and the evolution of colour constancy; ^[4]
- area V4 and selectivity for 'non-Cartesian' gratings; [5]
- IT cortex and response selectivity for abstract objects, and faces; [6-8]
- Different levels of categorization; population coding v. 'Grandmother Cells'.
- area V5 and response selectivity for pattern motion, and surface tilt; [9]
- area MST and response selectivity for components of optic flow (expansion, rotation).

Mechanisms for progressive implementation of object recognition in ventral visual pathway

- Computational model of ventral visual pathway using alternating 'simple' and 'complex' pooling of afferents to achieve specificity and invariance ^[10]
 - illustrated by selectivity for curvature, and curved boundary elements in V4; [11]
- Specialised 'face patches', in humans & macaques [12]
 - hierarchical development of view invariance, and selectivity for identity; ^[13]
 - cells with multiple face component selectivities: [14]

Forward versus backward pathways: the theory of 'predictive coding' (PCT)

- illusions that demonstrate the influence of prior knowledge upon perception;

- PCT interprets backward pathways to convey predictions, and forward pathways to carry error signals
 (see slides for a fuller exposition);
- Recent evidence for predictive responses in area V1 of the mouse ^[15]
- 'Precision': the computational quantity in PCT that controls the gain of the ascending error signal;
- Regulation of pyramidal neuron excitability by backward projecting axons terminating upon apical dendrites in layer 1 ^[16]

Basic reading

A Vision of the Brain

Zeki, Blackwell, Oxford 1993 chapter 23-26 on colour constancy and colour physiology

Inferotemporal cortex and object vision.

Tanaka Annual Review of Neuroscience, 19:109-139 (1996).

The distinct modes of vision offered by feedforward and recurrent processing.Lamme & RoelfsemaTrends in Neuroscience, 23: 571-579 (2000).

Cortical	<i>Structure and Function.</i> Shipp	Current Biology. 17: 443-449 (2007).	
Transfo	rmation of shape informati	on in the ventral pathway.	7 (2007)
	Connor et al.	Current Opinion in Neurobiology. 17: 140-	7 (2007).
Higher order visual processing in macaque extrastriate cortex.			
	Orban	Physiological Reviews. 88: 59-89 (2008).	
Parallel processing strategies of the primate visual system.			
	Nassi & Callaway	Nature Reviews Neuroscience 10, 360-372	(2009).
The importance of being hierarchical.			
	Markov & Kennedy	Current Opinion in Neurobiology 23:187-94	4 (2013).
Reflecti	ons on agranular architectu Shipp et al.	<i>ure: predictive coding in the motor cortex.</i> Trends in Neuroscience 36:706-16 (2013).	[- equally relevant to visual cortex]
Visual C	Dbject Recognition: Do We ((Finally) Know More Now Than We Did?	
Gauthie	uthier & Tarr Annual Review of Vision Science. 2: 377-396 (2016).		
Face Pro	ocessing Systems: From Ne	urons to Real-World Social Perception.	
Freiwal	eiwald <i>et al.</i> Annual Review of Neuroscience, 39: 325-346 (2016)		

Specific Sources

- 1. Felleman DJ, Van Essen DC (1991) *Distributed hierarchical processing in the primate cerebral cortex*. Cereb Cortex. 1: 1-47.
- 2. Peterhans E, von der Heydt R (1991) Subjective contours bridging the gap between psychophysics and physiology. Trends Neurosci. 14: 112-119.
- 3. Pan YX, Chen MG, Yin JP et al. (2012) Equivalent Representation of Real and Illusory Contours in Macaque V4. J Neurosci. 32: 6760-6770.
- 4. 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: 3047-3059.
- 5. Gallant JL, Connor CE, Rakshit S *et al.* (1996) *Neural responses to polar, hyperbolic, and Cartesian gratings in area* V4 of the macaque monkey. J Neurophysiol. 76: 2718-2739.
- 6. Tanaka K, Saito H, Fukada Y, Moriya M (1991) Coding visual images of objects in the inferotemporal cortex of the macaque monkey. J Neurophysiol. 66: 170-189.
- 7. Tanaka K (2003) Columns for complex visual object features in the inferotemporal cortex: clustering of cells with similar but slightly different stimulus selectivities. Cereb Cortex. 13: 90-99.
- 8. Desimone R, Albright TD, Gross CG, Bruce C (1984) *Stimulus selective properties of inferior temporal neurons in the macaque*. J Neurosci. 4: 2051-2062.
- 9. Born RT, Bradley DC (2005) Structure and function of visual area MT. Annu Rev Neurosci. 28: 157-189.
- 10. Cadieu C, Kouh M, Pasupathy A *et al.* (2007) *A model of V4 shape selectivity and invariance*. J Neurophysiol. 98: 1733-1750.
- 11. Pasupathy A, Connor CE (2001) Shape representation in area V4: position-specific tuning for boundary conformation. J Neurophysiol. 86: 2505-2519.
- 12. Tsao DY, Moeller S, Freiwald WA (2008) *Comparing face patch systems in macaques and humans*. Proc Natl Acad Sci U S A. 105: 19514-19519.
- 13. Freiwald WA, Tsao DY (2010) Functional compartmentalization and viewpoint generalization within the macaque face-processing system. Science. 330: 845-851.
- 14. Freiwald WA, Tsao DY, Livingstone MS (2009) *A face feature space in the macaque temporal lobe*. Nat Neurosci. 12: 1187-1196.
- 15. Fiser A, Mahringer D, Oyibo HK et al. (2016) Experience-dependent spatial expectations in mouse visual cortex. Nat Neurosci. 19: 1658-1664.

16. Larkum M (2013) A cellular mechanism for cortical associations: an organizing principle for the cerebral cortex. Trends Neurosci. 36: 141-151.