Introduction

- What is consciousness?

The physiological basis of subjective awareness remains a genuine scientific mystery (the 'hard' problem of consciousness) Definition of the function of consciousness;

Definition of the 'NCC'.

- Does visual consciousness equate to awareness of all information encoded in each area?
 - No, because some neural encodings demonstrably do not reach awareness:-
 - Destruction of V1 may leave residual 'blindsight' possibly contingent on LGN output bypassing V1^[1]
 - The existence of monocular neurons in V1;
 - \circ ~ V1 neurons whose spatial frequency sensitivity exceeds perceptual acuity $^{\![2]}$
 - Phenomena such as 'motion-induced blindness'^[3], 'change blindness' & 'inattentional blindness'.
 - Hence, the NCC concerns those neural encodings/operations that do result in awareness.

NCC may be classified by brain location...

The retina is outside the NCC:

• Hallucinatory perception possible within retinally blindfield (Charles Bonnet syndrome)^[4]

Is area V1 outside the NCC ? YES ! - as supposed by Crick & Koch (1995)^[5]

- YES (?) because V1 has no direct communication with frontal planning areas;
- YES (?) because monocular neurons in V1 do not give a percept of monocular stimulation.
- YES (?) because V1 wavelength tuned cells fail to correlate with colour percepts;
- YES (?) Blindsight 'Riddoch' syndrome, awareness of motion in the absence of visual sensation proper [6]
- YES (?) Absence of motion vision caused by V5 lesion, despite V1 being intact ^[7]
- NO (?) TMS to V1 modulates feedback from V5 & motion percept ^[8]
- YES (?) This is still an active debate (2011)... (awareness v non-awareness fails to modulate V1 activity)^[9]

The feedback hypothesis of NCC

- Theory of recurrent (or re-entrant) processing being the key ingredient of NCC (Lamme, 2006)
 - The time course of the neural activity in V1 correlating with correct detection of a target is consistent with an origin in feedback from higher areas ^[10]

The NCC as an experimental paradigm, or strategy

- Use of bistable percepts , e.g. binocular rivalry (BR)
 - o Bistable perceptual phenomena imply neural competition
 - \circ $\;$ Physiological phenomena correlating with bistable percepts may be part of NCC
 - Eye-switching experiment implies an important component of BR is 'image rivalry', in addition to eye rivalry [11]

Correlates of rivalry in BOLD signal (fMRI studies of human perception)

- Face v house paradigm reveals focus of activity switching between FFA and PPA ^[12]
- Vertical v horizontal grating reveals rivalrous activity in V1 (use blindspot to resolve ocular-specific activity)^[13]
- Higher resolution scan shows rivalrous activity in LGN, as well as V1^[14]

Correlates of rivalry in single unit activity

- Increasing proportion of bistable modulating neurons through areas V1, V4 and IT cortex; ^[15 16]
 - Also found in human hippcampal formation ^[17]
 - Note use of 'flash-suppression' version of rivalry
 - Single neuron activity recorded in monkey LGN not reported to modulate with rivalry [18]
 - Local Field Potential (LFP) signal recorded in V1 also modulates, at 'gamma' frequencies ^[19]
 - LFP is more analogous to BOLD signal recorded by fMRI

General Reading

Consci	<i>iousness and neuroscience.</i> Crick and Koch, Cerebral Cortex. 8: 97-107 (1998).
On the	e neural correlates of visual perception. Pollen, Cerebral Cortex. 9: 4-19 (1999).
The di	<i>isunity of consciousness.</i> Zeki, Trends in Cognitive Sciences. 7: 214-218. (2003).
Psycho	ophysical magic: rendering the visible 'invisible'. Kim and Blake, Trends in Cognitive Sciences. 9: 381-8 (2005).
Neura	<i>l bases of binocular rivalry.</i> Tong <i>et al.</i> , Trends in Cognitive Sciences. 10: 502-511 (2006).
Toward	ds a true neural stance on consciousness. Lamme, Trends in Cognitive Sciences. 10: 494-501 (2006).
Decodi	ing visual consciousness from human brain signals. Haynes, Trends in Cognitive Sciences. 13: 194-202 (2009).
Neuror	nal gamma-band synchronization as a fundamental process in cortical computation. Fries, Annual Review of Neuroscience. 32: 209-224 (2009).

Can binocular rivalry reveal neural correlates of consciousness? Blake et al. Philos Trans R Soc Lond B Biol Sci. 369: 20130211 (2014).

Neural correlates of consciousness: progress and problems. Koch *et al.* Nature Reviews Neuroscience 17: 307-321 (2016)

Website with abundant practical & theoretical information (& video) all regarding retinal rivalry: www.jove.com/details.stp?id=2030

Specific Sources

- 1. Schmid MC et al. (2010) Blindsight depends on the lateral geniculate nucleus. Nature. 466: 373-377.
- 2. He S, MacLeod DI (2001) Orientation-selective adaptation and tilt after-effect from invisible patterns. Nature. 411: 473-476.
- 3. Bonneh YS et al. (2001) Motion-induced blindness in normal observers. Nature. 411: 798-801.
- 4. ffytche DH (2009) Visual hallucinations in eye disease. Curr Opin Neurol. 22: 28-35.
- 5. Crick F, Koch C (1995) Are we aware of neural activity in primary visual cortex? Nature. 375: 121-123.
- 6. Ffytche DH, Zeki S (2011) The primary visual cortex, and feedback to it, are not necessary for conscious vision. Brain. 134: 247-257.
- 7. Shipp S et al. (1994) The brain activity related to residual motion vision in a patient with bilateral lesions of V5. Brain. 117: 1023-1038.
- 8. Silvanto J et al. (2005) Striate cortex (V1) activity gates awareness of motion. Nat Neurosci. 8: 143-144.
- 9. Watanabe M et al. (2011) Attention but not awareness modulates the BOLD signal in the human V1 during binocular suppression. Science. 334: 829-831.
- 10. Super H et al. (2001) Two distinct modes of sensory processing observed in monkey primary visual cortex (V1). Nat Neurosci. 4: 304-10.
- 11. Logothetis NK et al. (1996) What is rivalling during binocular rivalry? Nature. 380: 621-624.
- 12. Tong F et al. (1998) Binocular rivalry and visual awareness in human extrastriate cortex. Neuron. 21: 753-759.
- 13. Tong F, Engel SA (2001) Interocular rivalry revealed in the human cortical blind-spot representation. Nature. 411: 195-199.
- 14. Haynes JD et al. (2005) Eye-specific effects of binocular rivalry in the human lateral geniculate nucleus. Nature. 438: 496-499.
- 15. Leopold DA, Logothetis NK (1996) Activity changes in early visual cortex reflect monkeys' percepts during binocular rivalry. Nature. 379: 549-553.

- 16. Sheinberg DL, Logothetis NK (1997) *The role of temporal cortical areas in perceptual organization*. Proceedings of the National Academy of Sciences of the USA. 94: 3408-3413.
- 17. Kreiman G et al. (2002) Single-neuron correlates of subjective vision in the human medial temporal lobe. Proc Natl Acad Sci USA. 99: 8378-8383.
- 18. Lehky SR, Maunsell JH (1996) No binocular rivalry in the LGN of alert macaque monkeys. Vision Res. 36: 1225-3124.
- 19. Keliris GA *et al.* (2010) The role of the primary visual cortex in perceptual suppression of salient visual stimuli. J Neurosci. 30: 12353-12365.