Possible functions of cortical feedback in human vision

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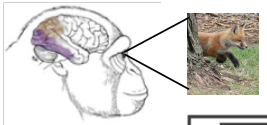
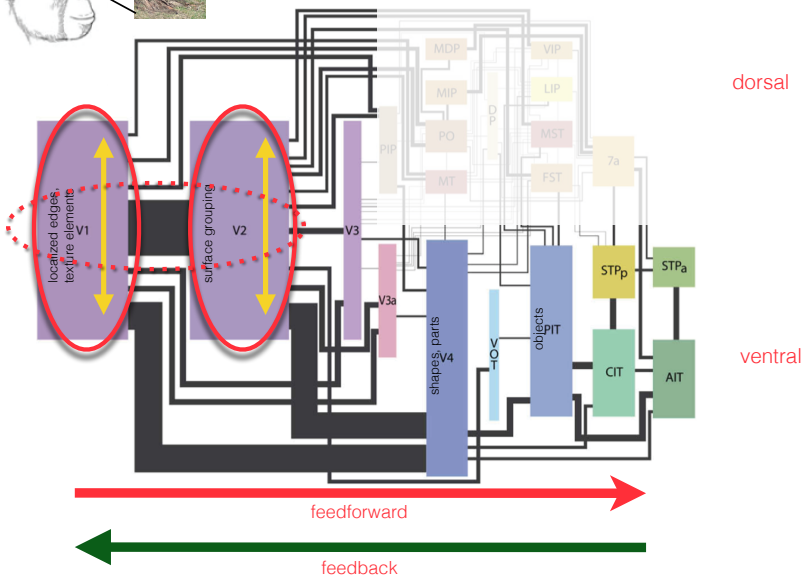
the remarkable flexibility of vision

one can see that there is an animal, a fox--in fact a baby fox. It is emerging from behind the base of a tree not, heading right, high-stepping through short grass, and probably moving rather quickly.

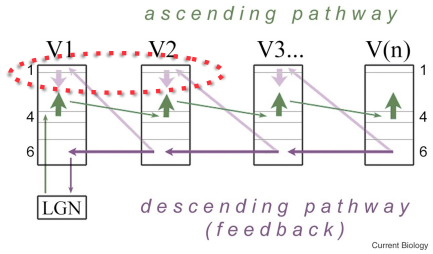
Its body fur is fluffy, relatively light in color, but with some variation. It has darker colored front legs and a dark patch above the mouth. Most of the body hairs flow from front to back. And what a cute smile, like a dolphin.

visual architecture that supports behavior





the anatomy shows systematic pattern of feedback circuitry

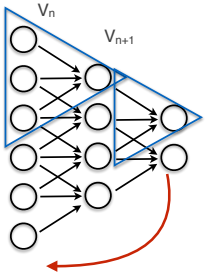


…and neurophysiology in monkeys and imaging studies in humans have shown the effects of attention, mental imagery, tactile tasks, and working memory on early visual areas

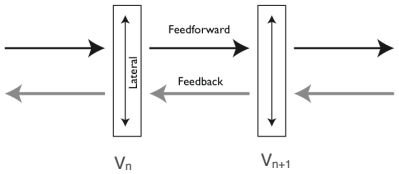
Markov, N. T., Vezoli, J., Chameau, P., Falchier, A., Quilodran, R., Huissoud, C., Lamy, C, Misery, P., Giroud,P., Ullman, S., Barone, P., Dehay, C., Knoblauch, K., and Kennedy, H. (2013). Anatomy of hierarchy: Feedforward and feedback pathways in macaque visual cortex. J Comp Neurol, 522(1), 225–259. http://doi.org/10.1002/cne.23458

experimental strategy in
human neuroimaging & psychophysics

look for effects of spatial context on local processing



problem: contextual information can be integrated feedforward, laterally within an area, and through feedback



possible functions of feedback between visual cortical areas

- selecting & amplifying streams of processing
- resolving local ambiguity using high-level knowledge
- binding information across levels of abstraction in the visual hierarchy
- accessing lower-level "expertise" as the task requires it, e.g. V1 for finer-grained spatial tasks

selecting & amplifying streams of processing for tasks

selective attention: spatial and feature-based

- "endogenous" attention—determined by task

  (in contrast to exogenous attention or bottom-up "saliency")

- "spotlight" metaphor — increasing "gain"

cf. Posner, M. I., & Gilbert, C. D. (1999). Attention and primary visual cortex. Proc Natl Acad Sci U S A, 96(6), 2585–2587.
Petersen, S. E., & Posner, M. I. (2012). The attention system of the human brain: 20 years after. Annual Review of Neuroscience, 35, 73.

resolving ambiguity using high-level knowledge

Perception as inference: "analysis-by-synthesis"

"predictive coding" as top-down error detection

- suppress lower-level responses to features "explained" by a higher-level interpretation

  and/or amplify those responses that are not "explained"

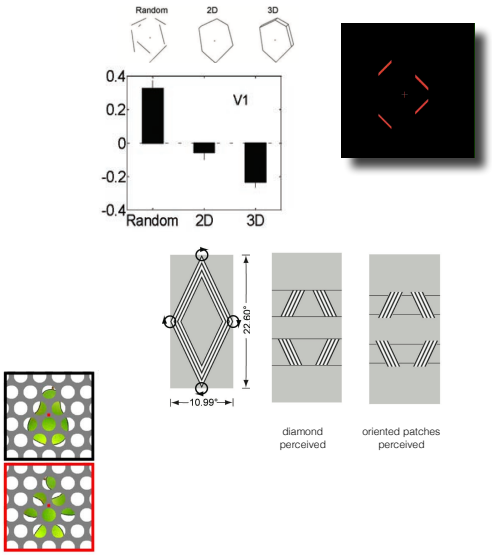
- top-down driven "automatic saliency"

cf. Mumford, 1992; Rao & Ballard, 1999

Bastos, A. M., Usrey, W. M., Adams, R. A., Mangun, G. R., Fries, P., & Friston, K. J. (2012). Canonical Microcircuits for Predictive Coding. *Neuron*, *76*(4), 695–711.

evidence for local, feature-specific feedback ?

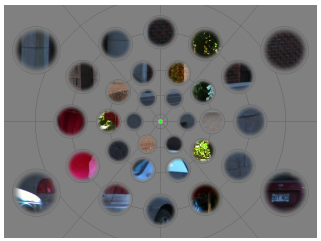
- fMRI has shown localized relative suppression in V1 to edges when edges appeared to be perceptually "well explained" by whole shape (Murray et al., 2002).
- human perceptual adaptation experiments show suppression to oriented lines—a local "feature"— when a whole shape is perceived. (He, Kersten, & Fang;2012)
- ultra-high resolution fMRI shows increased V1 activity to scrambled vs. whole shapes (Olman, Harel, Feinberg, He, Ugurbil, & Yacoub; (2012)



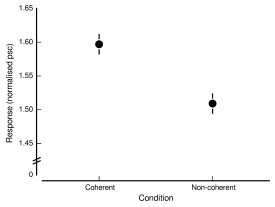
binding information across levels of abstraction

- amplify lower-level responses consistent with high-level a explanation
  - perhaps important given clutter
  - and/or subsequent tasks that involve decisions across spatial scale within an object
- top-down "sparsification"

cf. Grossberg & Mingolla, 1985; Ullman, S, 1995



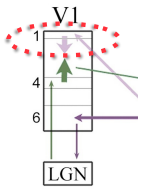
Mannion, D. J., Kersten, D. J., & Olman, C. A. (2015). Scene coherence can affect the local response to natural images in human V1.



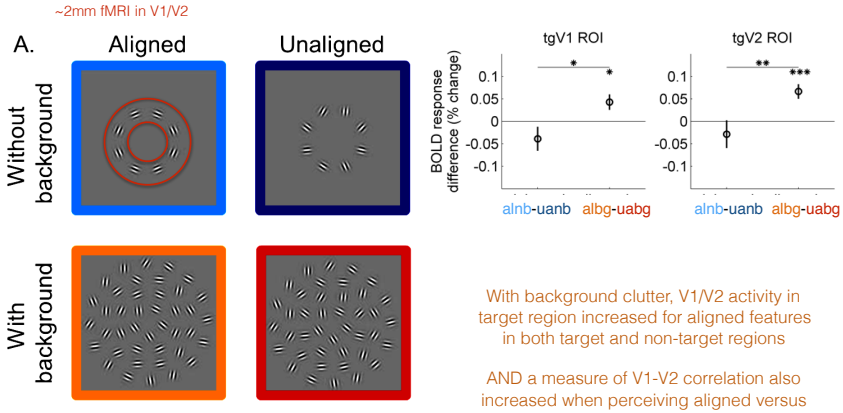
Larger fMRI responses to peripheral patches belonging to the perceived "coherent" image

Preference for coherent patches found in more superficial layers of V1

Muckli, L., De Martino, F., Vizioli, L., Petro, L. S., Smith, F. W., Ugurbil, K., Goebel, R. and Yacoub E. (2015). Contextual Feedback to Superficial Layers of V1.



localized enhancement of V1 & V2 voxel activity depends the complexity of the perceptual organization problem



With background clutter, V1/V2 activity in target region increased for aligned features in both target and non-target regions

AND a measure of V1-V2 correlation also increased when perceiving aligned versus unaligned contours.

Cheng Qiu, Philip Burton, Daniel Kersten, Cheryl A. Olman (in press, 2016) Responses in early visual areas to contour integration are context dependent. Journal of Vision

accessing lower-level "expertise"

hierarchically organized expertise

- Lee, T. S., Mumford, D., Romero, R., & Lamme, V. A. (1998); Hochstein, S., & Ahissar, M. (2002)

"executive metaphor" — in contrast to spotlight metaphor, emphasizes flexible computations

"spatial buffer hypothesis": for fine-grained spatial tasks—V1's "speciality" — Lee et al., 2002

are foveal cortical neurons "consulted" for the analysis of detail in the absence of direct stimulation?

evidence from psychophysics

Temporally flexible feedback processing in foveal cortex for peripheral object recognition. X Fan, L Wang, H Shao, D Kersten, S He (2016, under review)

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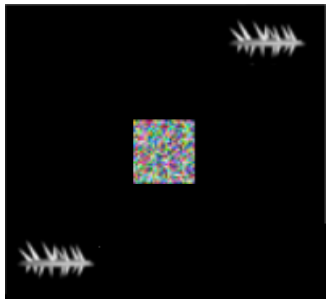
some background

- Voxels in non-stimulated V1 contain information about object category for within-category discriminations
  - Williams, M. A., Baker, Op de Beeck, H. P., Shim, W. M., Dang, S., Triantafyllou, C., & Kanwisher, N. (2008)
- Transcranial magnetic stimulation (TMS) pulse to foveal cortical areas most effective 350-400 msec after stimulus onset.
  - Chambers, C. D., Allen, C. P. G., Maizey, L. & Williams, M. (2013)
- Visual noise presented to fovea has a similar disruptive effect on task performance.
  - Yu Q & Shim WM (2016)



summary

- neuroimaging and psychophysics supports analysis-by-synthesis role for feedback for predictive coding and binding across hierarchy
  - effect of feedback to superficial layers of human V1 is measurable
- experiments on human fine-grain discrimination of peripherally viewed objects suggests that feedback isn't necessarily automatically engaged, but occurs when high-level area is ready for it.

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X Fan, L Wang, Y Han, Chinese Academy of Science
Fang Fang, Dongjun He, Peking U

Damien Mannion, U of New South Wales

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