Achromatic contrast adaptation in parasol and midget ganglion cells of the macaque monkey retina

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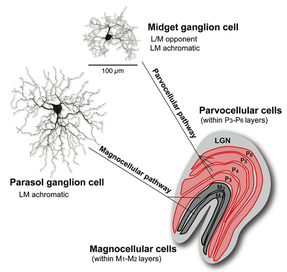
Abstract A0135

Background



Adaptation to temporal variation in light intensity, or contrast, is a fundamental property of the visual system and has been observed previously in mammalian retinal ganglion cells, including primate (Chander & Chichilnisky, 2001).

In the primate lateral geniculate nucleus (LGN), magnocelluar (LGNm) but not parvocellular (LGNp) relay cells showed contrast adaptation (Solomon et al., 2004). This result seems counterintuitive since the parvocellular pathway mediates achromatic spatial resolution and is critical for form perception (Lennie & Movshon, 2005).

Here, we measure contrast adaptation in identified LGNp-projecting midget and LGNm-projecting parasol retinal ganglion cells in a light adapted in vitro preparation of the macaque monkey retina for the first time.

Methods: Experimental design

Experiment 1: We measured spike responses as a function of the achromatic contrast for midget and parasol cells. We then compared the shape of contrast response function for both cell types by fitting with the Naka-Rushton function.

Experiment 2: We measured spike responses before, during and after exposure to high-contrast stimuli for both cell types, and then the effect of contrast adaptation was evaluated by:

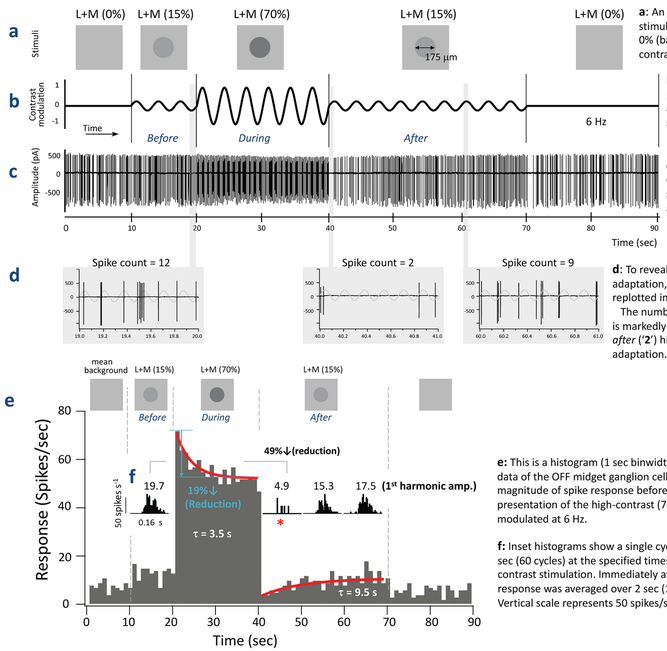
(1) comparing the magnitude of spike responses before, during and after high contrast adaptation.

(2) comparing the time constant (τ), revealing the ability of the cell to integrate visual input over time, by fitting spike data with an exponential function during and after high contrast adaptation.

For all experiments, achromatic contrast, stimulus configuration, and temporal frequency are varied.

Methods: Stimuli

All stimuli were L+M spots sinusoidally modulated in intensity around a fixed mean luminance at 4, 6 or 10 Hz temporal frequency. The small-field, full-field & surround stimuli were used for isolating the RF center, center + surround, & surround.



a: An example of the small-field stimuli (D = 175 µm) with the 0% (background), 15%, and 70% contrast, modulated at 6 Hz.

b: The adaptation protocol before, during and after high contrast stimulation.

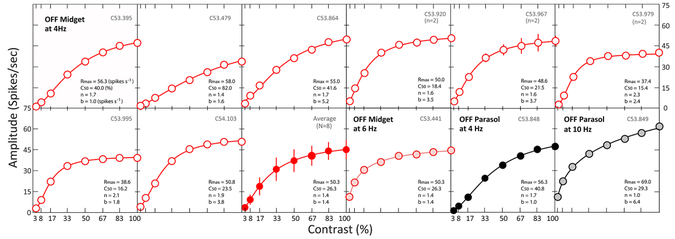
c: Raw spike data of an OFF midget ganglion cell, sinusoidally modulated at 6hz .

d: To reveal the effect of contrast adaptation, raw spike data (**c**) is replotted in small time windows. The number of spikes *before* ('**12**') is markedly reduced *immediately after* ('**2**') high contrast (70 %) adaptation.

e: This is a histogram (1 sec binwidth) of the raw spike data of the OFF midget ganglion cell (**b**): This reveals magnitude of spike response before, during, & after presentation of the high-contrast (70%) spot stimulus, modulated at 6 Hz.

f: Inset histograms show a single cycle averaged over 10 sec (60 cycles) at the specified times before & after high contrast stimulation. Immediately after adaptation (*) response was averaged over 2 sec (12 cycles). Note: Vertical scale represents 50 spikes/sec.

Result (1): Achromatic (L+M) contrast response functions (CRFs) in midget and parasol retinal ganglion cells



Note: Solid lines are for the Naka-Rushton function, $R(C) = R_{max} * (C^n/(C^n + C_{50}^n)) + b$, where R_{max} is the maximal response in spikes s^{-1}; C is the Michelson contrast; C_{50} is the contrast at half-maximum; n is the steepest slope of the contrast response function; b is the baseline response in spikes s^{-1}. (R_{max} C_{50} b & n are free parameters). The data are fitted with the Naka-Rushton function (solid lines) which provides a good fit to the spike data (the average R^2 values is 0.96). The average and individual fitted values are given.

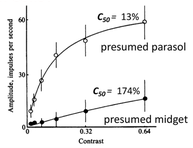
Summary

- Spike responses as a function of the L+M contrast for the midget (red circles) and parasol (black circles) cells are plotted at different temporal frequencies. The average across the 8 OFF midget cells is shown (solid red circles; center bottom plot). Error bars are ± 1*SD* of the mean.
- Both midget and parasol cells show the typical sigmoidal shaped contrast response. The shape and sensitivity of the contrast response function differs markedly from that found previously for presumed retinal midget cells (see the figure below from Kaplan & Shapley, 1986).
- An unexpected trend in this data is that midget cells reach saturation more quickly than parasol cells, although the variability across the cells is large: the fitted values of 'C_{50}' for the midget cells are smaller than those for the parasol cells, but the fitted values of '***n***' for the midget cells are larger than those for the parasol cells (Midget: C_{50} = 30% ±7.9*SE*; ***n*** = 1~2.26, Parasol: C_{50} = 35% ±5.7*SE*; ***n*** = 1.0~1.7).

low contrast sensitivity in midget ganglion cells?

• The shape and sensitivity of the contrast response function we found differs markedly from that found previously for presumed midget cells (Kaplan & Shapley, 1986, their Fig. 2).

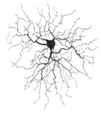
• The presumed parasol cells showed a steeply rising response to contrast and then saturated, but the presumed midget cells were unresponsive at low contrasts with a shallow linear increase over the entire contrast range.



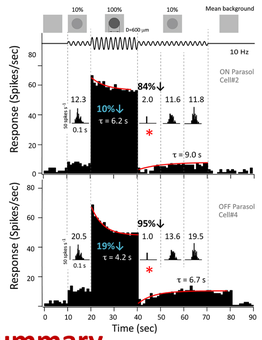
Average contrast response functions for 36 S potentials (synaptic potentials recorded in LGN relay cells derived from summed ganglion cell input) recorded from one rhesus monkey: 28 recorded in the LGNp and 8 recorded in LGNm layers.

The stimulus was sinusoidal grating of optimal spatial frequency for each cell, drifting at 4 Hz.

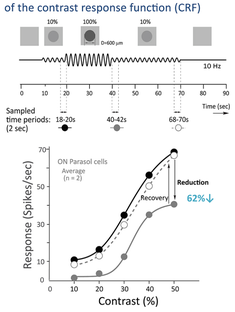
Result (3): Achromatic (L+M) contrast adaptation in parasol ganglion cells



a. Small-field stimulus (covering the RF center only)



b. Contrast adapation effect in the shape of the contrast response function (CRF)



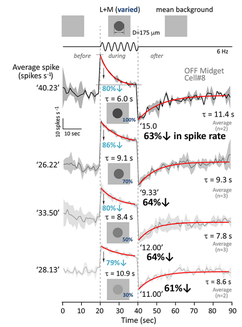
Note: Solid and dashed lines show the best-fitting predictions of the Naka-Rushton function (see above; the average R^2 value is 0.98).

Summary

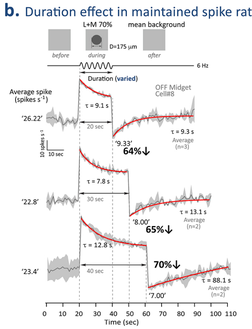
- (**a**) Two parasol cells show substantial contrast adaptation in the spike rate during and after high contrast stimulation. During adaptation, the spike rate declined by **14.5%** (±6.4*SD*), with a time constant of **5.2s** (±1.4*SD*). Immediately after adaptation, the spike rate is significantly reduced by **89.5%** (±7.8*SD*) and recovers with a time constant of **7.9s** (±1.6*SD*).
- (**b**) The spike rate as a function of contrast before (black circles), immediately after (gray circles) and after longer recovery (open circles). Spike rate declined by **62%** (±23*SD*) immediately after adaptation period and recovered to pre-adaption levels (open circles).

Result (2): Achromatic (L+M) contrast adaptation in midget ganglions cells

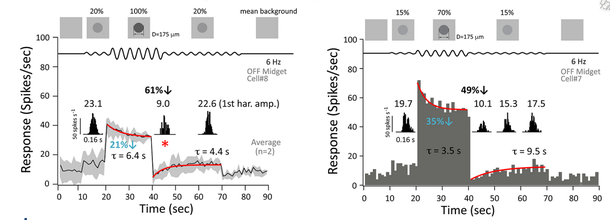
a. Contrast effect in maintained spike rate



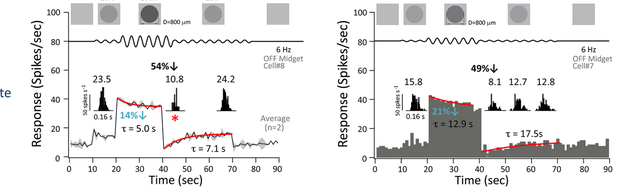
b. Duration effect in maintained spike rate



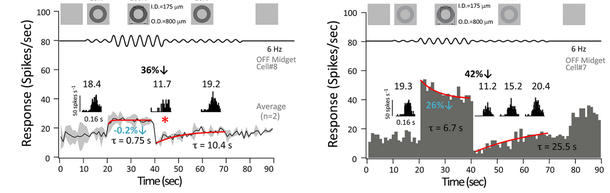
c. Small-field stimulus (covering the RF center only)



d. Full-field stimulus (covering the entire RF)



e. Surround stimulus (covering the surround but not the RF center)



Summary

- Contrast adaptation in the maintained spike rate with respect to the stimulus contrast (**a**) and its duration (**b**).
  - (**a**) An OFF midget cell shows significant contrast adaptation in maintained spike rate during and after high contrast stimulation. During adaptation, the spike rate declined by **81.7%** (±3.2*SD*), with a time constant of **8.6s** (±2.0*SD*) across different conditions. Immediately after adaptation, the maintained spike rate at the mean background is reduced by **63%** (±1.4*SD*) across different adaptation contrasts. The maintained rate recovers with a time constant of **9.3s** (±1.5*SD*).
  - (**b**) Increasing the high contrast adaptation period from 20 to 40 seconds appeared to produce a slightly increasing effect, from 64-70% on the reduction in maintained spike rate.
- Contrast adaptation in the spike rate with respect to the different stimulus types (small-field (**c**), full-field (**d**) and surround (**e**)).
  - (**c-e**) For all stimulus types, two midget cells show strong contrast adaptation in spike rate during and after high contrast adaptation. During adaptation, the spike rate declined by **22.8%** (±8.8*SD*), with a time constant of **7.0s** (±4.1*SD*) for the small- and full-field conditions (**c-d**), but for the surround condition (**e**) the variability is large across the cells. Immediately after adaptation, the spike rate to the low contrast (15-20%), is reduced by **55%** (±8.5*SD*) for the small-field (**c**), **52%** (±3.5*SD*) for the full-field (**d**) and **39%** (±4.2*SD*) for the surround (**e**).

Conclusions

1) The shape and high sensitivity of the contrast response function for midget cells we show here is comparable to that for parasol cells but differs markedly from the linear low sensitivity found previously for presumed midget ganglion cells recording S potentials in LGN relay cells (Kaplan & Shapley, 1986).
2) Unlike the previous report for LGN relay cells where contrast adaption was restricted to LGNm cells, we find significant achromatic contrast adaptation for parvocellular projecting midget cells – even at relatively low adapting contrasts – comparable to that for the magnocellular projecting parasol cells.
3) We conclude that the high achromatic contrast sensitivity and strong contrast adaptation found for midget ganglion cells is consistent with a fundamental role for the parvocellular pathway in achromatic spatial vision (Wool et al., 2018).

References

1. Chichilnisky, E.J. & Chander, D. (2001). J. Neurosci. *21*(24):9904-9916.
2. Lennie, P. & Movshon, J.A. (2005). J. Opt. Soc. Am. A. *22*:2013-2033.
3. Solomon, S.G., Peirce, J.W., Dhruv, N., & Lennie, P. (2004). Neuron. *42*:155-162.
4. Kaplan, E. & Shapley, R.M. (1986). Proc. Natl. Acad. Sci. *83*:2755-2757.
5. Wool, L.E., Crook, J.D., Troy, J.B., Packer, O.S., Zaidi, Q., & Dacey, D.M. (2018). J. Neurosci. *38*(6):1520-1540.