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# Neuronal and Perceptual Differences in the Temporal Processing of Darks and Lights

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## SUMMARY

**Visual information is mediated by two major thalamic pathways that signal light decrements (OFF) and increments (ON) in visual scenes, the OFF pathway being faster than the ON. Here, we demonstrate that this OFF temporal advantage is transferred to visual cortex and has a correlate in human perception. OFF-dominated cortical neurons in cats responded ~3 ms faster to visual stimuli than ON-dominated cortical neurons, and dark-mediated suppression in ON-dominated neurons peaked ~14 ms faster than light-mediated suppression in OFF-dominated neurons. Consistent with the neuronal differences, human observers were 6–14 ms faster at detecting darks than lights and better at discriminating dark than light flickers. Neuronal and perceptual differences both vanished if backgrounds were biased toward darks. Our results suggest that the cortical OFF pathway is faster than the ON pathway at increasing and suppressing visual responses, and these differences have parallels in the human visual perception of lights and darks.**

## INTRODUCTION

Neurons in the visual pathway have different response time courses, which are likely to serve different functions. In cat, the fast, transient visual responses of Y thalamic cells are thought to be suitable for encoding motion, whereas the longer and more sustained responses of X cells are better suited to encode form (Derrington and Fuchs, 1979; Lehmkuhle et al., 1980; Sherman and Spear, 1982; Demb et al., 2001). In contrast to X and Y visual pathways, ON and OFF pathways were originally thought to have similar response time courses and differ only in their preferences for contrast polarity, with ON neurons responding to light increments and OFF neurons to decrements (Hartline, 1938; Kuffler, 1953). This understanding of ON and OFF pathways in visual function has been changing over the past decades as new functional differences between the two emerge (Zemon et al., 1988; Chichilnisky and Kalmar, 2002; Zaghloul et al., 2003; Jin et al., 2008; Yeh et al., 2009; Liang and Freed, 2010; Pandarinath et al., 2010; Xing et al., 2010; Jin et al., 2011; Hesam Shariati and Freeman, 2012). There is evidence that OFF neurons respond faster to visual stimuli than ON neurons in the retinae of salamanders, turtles, and mice (Baylor and Fettiplace, 1977; Copenhagen et al., 1983; Burkhardt et al., 1998, Burkhardt, 2011; Gollisch and Meister, 2008; Nichols et al., 2013) and in the visual thalamus of cats (Jin et al., 2011).

The difference in response time courses between ON and OFF pathways most likely originates in retinal bipolar cells that use slow metabotropic glutamate receptors (mGluR6) to generate ON responses and fast ionotropic receptors to generate OFF responses (Nakajima et al., 1993; Snellman et al., 2008; Koike et al., 2010). While these temporal differences seem to be preserved in the thalamocortical pathway (Jin et al., 2011), it remains unclear if they are transferred to visual cortex and influence perception. Because neurons in layer 4 of primary visual cortex receive convergent inputs from both ON and OFF thalamic cells (Tanaka, 1983; Reid and Alonso, 1995; Alonso et al., 2001), the thalamocortical convergence could remove the ON-OFF temporal differences imposed by the receptor kinetics in the retina. Alternatively, the thalamocortical convergence could preserve or even amplify the temporal differences, creating a temporal asymmetry in the perception of darks and lights. By taking advantage of multielectrode recordings, we demonstrate that ON-OFF temporal differences are not only present in primary visual cortex but are likely amplified by thalamocortical convergence and intracortical suppression (Hirsch et al., 1998; Hirsch, 2003). Moreover, by using psychophysical measurements of temporal thresholds, we demonstrate that humans process darks 6–14 ms faster than lights, a temporal difference that is remarkably close to our physiological measurements of temporal differences in ON and OFF pathways. We also show that both temporal differences, in ON-OFF neuronal response latency and dark-light detection, vanish if the background is adjusted to compensate for the irradiation illusion, in which light stimuli on dark backgrounds appeared larger than physically equal dark stimuli on light backgrounds (Galilei, 1632). Finally, we show that dark-mediated cortical suppression is stronger and faster than light-mediated cortical suppression, and consequently, human observers take longer to perceive a stimulus after a light turns to dark than after a dark turns to light. These findings have important implications for our understanding of the functional organization of ON and OFF visual pathways and the perception of darks and lights in human observers.

 

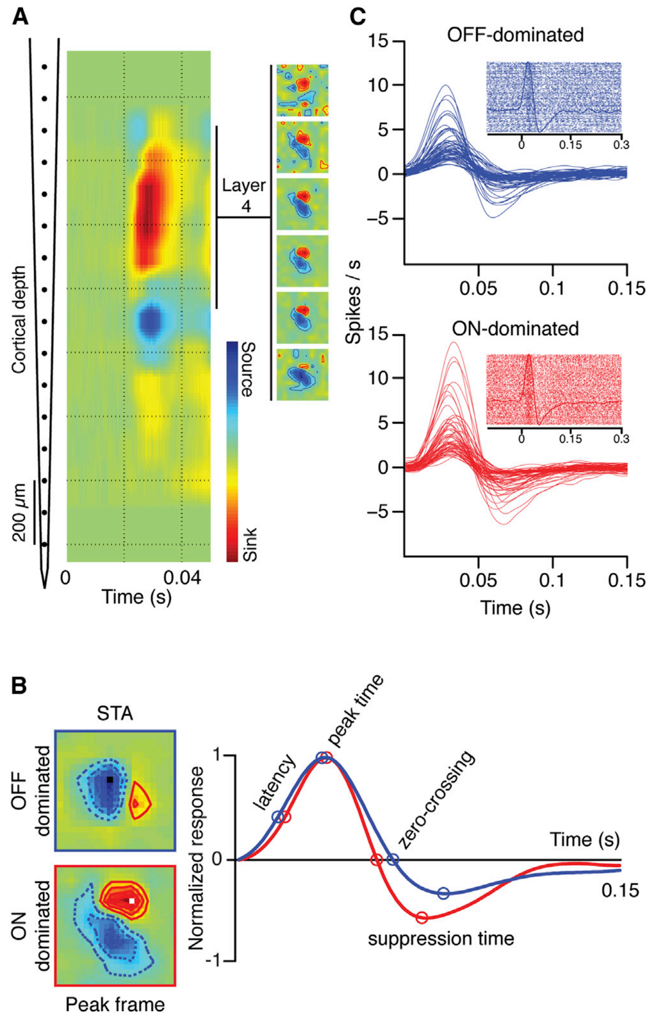


**Figure 1. Recordings from Cortical Layer 4 in Anesthetized Cats**

Multiple penetrations were made using a 16-channel probe (interelectrode distance of 100 μm) in V1 of cat visual cortex. The RFs were mapped using binary white noise stimuli.

(A) The depth of cortical layer 4 was identified as a strong current sink generated by a full-field flash presented at time 0 (left). Cortical RFs were measured in layer 4 with binary white noise by spike trigger averaging (STA) the stimulus (right).

(B) The white noise pixel that generated the strongest response was used to determine the dominance polarity of the cortical RF (light for ON dominated, and dark for OFF dominated). Four time points (latency, peak time, zero crossing, and suppression time) were chosen to compare the temporal dynamics.

(C) The time stamps of the white noise frames with the pixel that generated the strongest response were used as triggers to generate peristimulus time histograms (PSTHs) and rasters for OFF-dominated (blue) and ON-dominated cells (red). The PSTHs were calculated with a 1 ms bin and smoothed using a moving average triangular filter of 21 ms width.

## RESULTS

A 16-channel multielectrode array was vertically introduced in cat visual cortex to record multiunit and single unit activity from cortical layer 4 (Figure 1A, left). Layer 4 was identified by current source density analysis (Jin et al., 2011), and the cortical receptive fields (RFs) were mapped with binary white noise stimuli by spike-trigger averaging (STA) the stimulus (Figure 1A, right inset). Each multiunit RF in cortical layer 4 was classified as OFF dominated (n = 418) or ON dominated (n = 220) by measuring the contrast polarity of the stimulus pixel that generated the maximum response at the peak frame (Figure 1B; ON shown in red; OFF shown in blue). We recently demonstrated that visual response latencies are ~3 ms shorter in OFF than ON X cells of the lateral geniculate nucleus (Jin et al., 2011), which are the main thalamic inputs to cat area 17 (Ferster, 1990). Because ON and OFF pathways converge in layer 4 cortical neurons, the ON-OFF latency differences could be reduced, preserved, or amplified by intracortical processing. Our results support the notion that the ON-OFF temporal differences are amplified in cortex and influence visual perception.

### Time Courses of ON and OFF Responses in Visual Cortex

To measure the latency differences between ON-dominated and OFF-dominated cortical neurons, we first selected the RF pixel that generated the maximum response in the RF map: the preferred stimulus pixel. The preferred stimulus pixel was dark for OFF-dominated and light for ON-dominated neurons (position and polarity illustrated by small dark and light squares in Figure 1B, left). We then used the time stamps of the white noise stimulus frames with the preferred pixel as stimulus onset to generate peristimulus time histograms (PSTHs). The number of white noise frames with the preferred stimulus pixel was approximately half of the entire white noise sequence (32,767 white noise frames); therefore, we generated a PSTH from ~16,383 spike rasters (Figure 1C). As shown in this PSTH, the onset of the preferred white noise pixel generates an increase in firing rate (peak) followed by a reduction in firing rate below baseline (suppression), as the preferred pixel reverses polarity (Figures 1B and 1C). The PSTHs revealed a great diversity of response magnitudes and time courses in both ON- and OFF-dominated cortical neurons (Figure 1C).

Similar to the properties of thalamic neurons, the response latency for cortical neurons was 3.45 ± 0.48 ms faster in OFF-dominated than in ON-dominated cortical sites ($p < 0.001$) (Figure 2A). However, unlike the thalamus, the ON-OFF temporal difference was not significant at the response peak (0.83 ± 0.54 ms; $p = 0.15$) and was reversed at the zero crossing with the baseline (7.52 ± 0.96 ms; $p < 0.001$), with the reversal reaching its maximum during the response suppression (13.99 ± 1.64 ms; $p < 0.001$; see distributions of temporal parameters in Figure S1, available online).

When presented in an ON subregion, a light spot followed by a dark spot generates an increase in firing rate (peak) followed by a reduction in firing rate below baseline (suppression). To measure the relative amplitudes of peak and suppression, we used two different indices: the amplitude ratio (AR) and the integral ratio (IR) of response suppression to response peak (see Experimental Procedures). Both indices were 1 when response peak and response suppression were equal and less than 1 when the suppression was smaller than the peak. Consistent with previous measurements in retinal ganglion cells and thalamic neurons (Zaghloul et al., 2003; Jin et al., 2011), the response