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Spotlight

Darks and Lights, the 'Yin–Yang' of Vision Depends on Luminance

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We all know the disappointment when, after a wonderful snapshot, the details in the photo are at much lower contrast than seen before with our own eyes. A recent study by Rahimi-Nasrabadi *et al*. revealed that this is because human vision accounts for actual luminance range and for accompanied asymmetric changes in dark and light contrasts.

How can neuronal processing do a better job sampling visual contrast in natural scenery than a high-tech camera? Throughout the day we experience changes in the amount of reflected light (i.e., luminance) that can range up to 10 000-fold. It has been generally assumed that in naturalist settings, luminance contrast (the relative difference in brightness of objects) is largely independent of luminance range. Accordingly, it has been commonly hypothesized that the mechanisms operating in the visual system aim to ensure that contrast sensitivity should become independent of absolute luminance. This, together with mechanisms that compensate for light intensity (e.g., pupil size changes), has been the mainstream line of thought in relation to the ability of biological systems to adjust to a wide range of luminance changes. Based on somewhat similar reasoning, cameras foremost use aperture width and shutter speed to handle variations in overall luminance. Because visual contrast often specifies the most informative parts within an image, sensitivity to contrast is fundamental for finding structure in the environment. In fact, up to now, also in the context of cortical visual processing, a prevalent notion has been that contrast sensitivity is essentially independent of luminance range [1].

A recent study from Jose-Manuel Alonso's group, Rahimi-Nasrabadi *et al*., [2] shows that this proposition is largely wrong. Thus, their findings may extend and revise current understanding of a widely accepted neuronal processing principle. Why were alternative accounts overlooked so far? The study is one of those cases where previous claims, especially those that appear set in stone, get disproved when revisited with newly available techniques and approaches [2]. First, to mimic contrast–luminance interactions in environments much brighter than typically used in laboratory settings, the authors employed a type of monitor for stimulus display that could reach exceptionally high luminance values. Second, the authors designed visual stimuli (as described next) that differ from the grating stimuli typically used for determining cortical contrast sensitivity. Importantly, the use of grating stimuli (i.e., patterns with symmetric deviations of white and black from mean luminance) hinders sampling of asymmetries between darks and lights (but see [3]).

In their study, Rahimi-Nasrabadi *et al*. used stimuli with different combinations of contrast polarity, luminance contrast, background luminance, and luminance range, while measuring neuronal responses across primary visual cortex in cats (using single-unit recordings) and in humans [using electroencephalogram (EEG)]. The authors found that increasing luminance led to a shift of the contrast response function for pathways signaling light ('ON' responses). This resulted in elevated sensitivity at lower light contrasts, at the cost of saturation at higher contrasts. Conversely, responses of pathways signaling darks ('OFF') became slightly more linearized. Taken together, these changes in the contrast response functions enhanced light–dark differences across the full range of contrasts. Consequently, on a sunny day, differences between the brightest regions of a scene appear less pronounced (Figure 1, left), while subtle dissimilarities within darker regions become more detectable (Figure 1, right).

Does such processing strategy make sense in terms of real-world vision? It does indeed. To examine this, the authors analyzed thousands of natural images that were carefully calibrated [4] such that original luminance values can be retrieved by conversion factors based on camera aperture, shutter time, and ISO number (see http://bethgelab.org/datasets/vanhateren/ for an online access of the dataset with convenient programming code). The analysis showed a striking similarity between the cumulative density functions of pixels categorized by either light or dark and the observed neuronal contrast response functions. Hence, neuronal function matched perfectly with visual input statistics. That is, asymmetries between dark and light distributions in natural images were mirrored by asymmetric deflections of the neuronal dark–light contrast response functions. Once more, these results demonstrate the remarkable ability of the visual system to efficiently encode and dynamically adapt to information content of natural habitats.

ON–OFF contrast asymmetries in the visual cortex are likely inherited from the retina [5]. The question of whether ON–OFF pathways remain segregated or alternatively merge at the cortical level has been a matter of some debate. While the two pathways are often thought to merge in the cortex, several studies by Jose-Manuel Alonso and colleagues demonstrated that the functional segregation of these pathways is preserved [5,6]. Relatedly, functional asymmetries between ON and OFF channels could explain why black letters written on white paper can be detected with higher resolution than vice versa [5]. Moreover, asymmetric processing of lights and darks preserves information about object contrast polarity [3] and may also support cortical

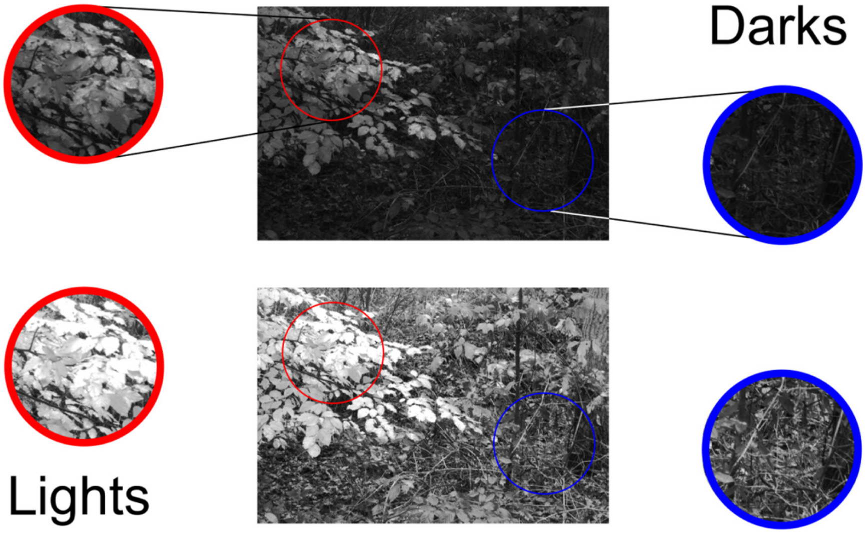

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Figure 1. Mimicking Human Vision. Efficient neuronal encoding of luminance contrast under largely different conditions of reflectance. Upper photograph shows an original image displayed as taken by a camera [4]. Bottom photograph is the same as upper photograph after applying an 'ONOFF' algorithm developed by Rahimi-Nasrabadi *et al*. based on responses in primary visual cortex (see also supplemental Figure 4 in [2]). Note that the algorithm simulating human perception slightly blurs contrast within bright regions (compare upper and lower left patches). Conversely, items within darker regions are perceived in much greater detail than within the original picture (*cf.* patches at right).

detection of motion [7]. In fact, similar computations of contrast polarity have been observed in humans and a wide range of species, including flies, suggesting an evolutionary well conserved (and therefore likely efficient) strategy for the detection of motion in natural surrounds [8].

Interestingly, despite considerable differences in recording methods across species (EEG versus single-cell recordings in humans versus cats, respectively), the study by Rahimi-Nasrabadi *et al*. yielded remarkably similar results for the two species investigated. This may simply point to obvious similarities in the experienced visual world of both species, despite discrepancies in the amount of day/night activities and the associated differences in luminance exposure. But perhaps an even more important point to consider is that the recordings in cats were performed under anesthesia. This may indicate that most of the neuronal image processing principles found in the study, which ultimately serve to drive attention and which are generally important for cognition, reflect subconscious 'automatic' computations.

The neuronal mechanisms by which the discovered luminance-dependent changes in the contrast response functions are brought about remain to be further explored. Possible contributors to such dynamics are modulatory systems. From sunrise to sunset, luminance values exhibit dramatic changes and the influence of some neuromodulators appears to covary with daily cycles as well. For example, release of serotonin seems to synchronize with the day–night cycle. Indeed, modulations of the contrast response function were recently shown to depend on serotonergic levels and the current state of the cortex [9]. As a number of psychiatric disorders (like depression, anxiety, and schizophrenia) are associated with serotonin-dependent changes in cortical state, one may speculate that measurements of dark–light contrast sensitivity that take luminance range into account may offer new approaches for diagnosis.

Along with implementations in image processing devices and of algorithmic tools that mimic more truthfully human luminance vision, the study by Rahimi-Nasrabadi *et al*. will certainly facilitate the characterization and monitoring of dysfunction associated with visual diseases. Furthermore, this line of research has significant potential in revealing the concrete neuronal causes of visual disorders. For instance, amblyopia, a severe asymmetric decline of visual cortical function (where input of one eye dominates input from the other eye; up to 5% of children worldwide are affected) was shown to correlate with optical blur during brain development and was associated with increasing dominance of the pathways signaling darks [10].

Yin and Yang are two complementary forces in ancient Chinese philosophy that together describe the nature of real-world elements. Yin represents the dark (negative) side, whereas Yang stands for the light (positive) one. In such figurative sense and in neuronal terms, the study by Rahimi-Nasrabadi *et al*. shows how light and dark forces interact and how such interactions profit from a third force, namely, luminance.

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Declaration of Interests

The author declares no competing interests in relation to this work.

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