

OFF RESPONSE (OFF RESPONSE)

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1. Core Definition and Functional Role

The **Off Response** is a fundamental physiological phenomenon observed in the visual system, defined specifically as the rapid depolarization of a neuron in reaction to the cessation or decrement of light stimulation. This reaction is contrary to the typical response seen when light is introduced. Functionally, the off response is essential for coding darkness, shadows, and the trailing edge of moving stimuli. It ensures that the visual cortex receives precise information not only about what is illuminated, but critically, about where illumination ends, allowing for robust processing of contrast and boundaries in the visual scene.

In classical neurophysiological terms, the off response is the transient burst of action potentials generated by specific visual neurons--often retinal ganglion cells, lateral geniculate nucleus (LGN) cells, and cells in the visual cortex--immediately following the transition from a state of illumination to darkness. This mechanism contrasts sharply with the **On Response**, which is characterized by depolarization and spiking activity upon the onset or increment of light. The segregated processing of light increments (On) and light decrements (Off) is a foundational principle of visual encoding, suggesting that the brain treats increases and decreases in luminance as fundamentally distinct pieces of information necessary for environmental interpretation.

The primary cells exhibiting this behavior are known descriptively as **Off Cells**. These neurons possess receptive fields where the central area is highly sensitive to the removal of light. As the source definition confirms, the off response is inherently tied to light reduction; it "do not occur when lights are brightened." This specificity underscores the efficiency of the visual system, dedicating distinct neural pathways to process changes in luminance contrast, thereby enhancing sensitivity to edges and movement, regardless of the overall illumination level of the environment.

2. Neurobiological Mechanism in the Retina

The genesis of the off response occurs primarily within the complex circuitry of the retina. The crucial differentiation between On and Off pathways takes place at the first synapse between photoreceptor cells (rods and cones) and the bipolar cells. Photoreceptors hyperpolarize (become more negative, inhibiting glutamate release) in response to light, and depolarize (increasing glutamate release) in the dark. The response of the downstream bipolar cells dictates the pathway.

In the case of the Off pathway, the signal transmission is direct and excitatory. Off-bipolar cells possess Glutamate receptors of the ionotropic type (iGluRs), typically AMPA or Kainate receptors. These receptors are excitatory. In the dark, photoreceptors release a high steady concentration of

glutamate. This glutamate excites (depolarizes) the Off-bipolar cell. When light is turned on, the photoreceptor hyperpolarizes, glutamate release drops, and the Off-bipolar cell hyperpolarizes and ceases firing. When the light is suddenly extinguished, the photoreceptor depolarizes rapidly, glutamate release surges back to baseline, causing the Off-bipolar cell to experience a strong, transient **depolarization** which initiates the off response spike train.

This direct excitatory action means that Off-bipolar cells are actively signaling the presence of darkness. They are excited by high glutamate levels (dark) and inhibited by low glutamate levels (light). This physiological characteristic provides the neural substrate for the subsequent Off-cells (retinal ganglion cells and beyond) to fire robustly only when the light stimulus ceases. The precise timing and intensity of this depolarization are crucial for encoding high-frequency changes in the visual input, particularly important for movement detection.

3. Receptive Field Organization of Off Cells

The functional segregation of On and Off responses is tightly integrated with the spatial organization of the receptive field. Off cells, particularly the **Off-Center Retinal Ganglion Cells**, exhibit a classical center-surround antagonistic organization, a feature essential for spatial filtering and contrast enhancement.

For an **Off-Center Cell**, the core of the receptive field is excitatory to light decrement. This means that turning a spot of light off within the center region causes the cell to fire vigorously. Conversely, turning a light on in the center inhibits the cell's baseline firing rate. The surrounding annular area of the receptive field operates in opposition: light decrement in the surround inhibits the cell, while light increment in the surround excites it. This antagonistic layout is fundamental for enhancing contrast detection, preventing the cell from responding equally to uniform illumination changes across a large area.

The critical utility of the off response, especially within this center-surround framework, is the precise localization of edges. When a boundary between light and dark falls across the receptive field, the off response component strongly emphasizes the dark side of the boundary. By having parallel On-Center and Off-Center pathways, the visual system ensures that every contrast boundary is doubly coded: the On-Center cell fires vigorously at the bright side of the edge, while the Off-Center cell fires vigorously at the dark side. This redundancy and complementarity drastically improves the reliability and spatial acuity of contrast processing.

4. Ascending Pathways and Cortical Processing

The distinction between On and Off signals is maintained throughout the central visual pathways, demonstrating its evolutionary and functional significance. Axons from the Off-Center Retinal Ganglion Cells project primarily to the Lateral Geniculate Nucleus (LGN) of the thalamus, the major

relay station for visual information before it reaches the cerebral cortex.

Within the LGN, the segregation is strictly maintained. Specific layers or sublaminae of the LGN are dedicated solely to receiving and relaying Off signals, while others handle On signals. This organization ensures that when the signal reaches the primary visual cortex (V1), the distinction between light increment and light decrement remains pristine. This input is crucial for the subsequent construction of orientation and direction selectivity observed in V1 neurons.

In V1, simple cells integrate inputs from multiple aligned LGN cells. These simple cells are often highly sensitive to either On or Off stimuli, or combinations thereof, placed in specific spatial arrangements. For instance, some simple cells respond optimally to a dark bar (Off stimulus) oriented at a particular angle against a light background, while others respond best to a bright bar (On stimulus). The precise integration of the off response, therefore, directly underpins the ability of the cortex to detect contours, motion, and complex spatial features.

5. Role in Temporal Resolution and Motion Detection

The **Off Response** is intrinsically linked to the temporal resolution of the visual system. Unlike the sustained firing characteristic of some P-type (parvocellular) retinal cells, the off response is often highly transient, characterized by a sharp burst of activity that quickly decays. This transient nature is particularly prominent in M-type (magnocellular) pathways, which are responsible for processing motion and coarse depth information.

The swift onset and decay of the depolarization upon light removal provide the system with the necessary speed to track rapidly changing stimuli. When an object moves across the visual field, the off responses generated at the trailing edge of the object provide rapid, sequential signals that allow the brain to calculate the object's velocity and trajectory. A defective or sluggish off response pathway would severely impair the capacity for smooth pursuit and reaction time, making it difficult to navigate dynamic environments.

Furthermore, the high contrast gain associated with the off pathway allows for effective signaling even when the change in luminance is small, provided the change occurs rapidly. This sensitivity to rapid decrements is hypothesized to be critical for survival behaviors, such as detecting sudden shadows cast by predators, where speed and reliability of darkness signaling are paramount.

6. Historical Context and Discovery

The initial observations leading to the concept of the off response predate sophisticated cellular recordings. Early electrophysiological work in the 1930s on the optic nerve, particularly by H.K. Hartline, demonstrated that visual neurons did not simply mimic the light stimulus but actively encoded changes. Hartline categorized neurons based on their firing patterns in response to light

steps: those that fired only when the light came on ("On fibers"), those that fired only when the light went off ("Off fibers"), and those that responded to both ("On-Off fibers").

The profound functional significance of the Off pathway was cemented by the subsequent work of Stephen Kuffler, who, working with cat retinas in the 1950s, meticulously mapped the receptive fields of retinal ganglion cells. Kuffler's discovery of the center-surround antagonism conclusively showed that the visual system segments inputs into dedicated channels, confirming that the off response was not merely an artifact of neural recovery but a crucial, actively constructed signal for detecting negative contrast.

Later work by David Hubel and Torsten Wiesel extended these concepts to the cortex, showing how the segregated On and Off inputs from the LGN were combined to generate the complex responses of cortical cells. Their findings confirmed that the off response is not simply a secondary inhibitory signal but an independently processed excitatory pathway, fundamental to all subsequent visual processing stages.

7. Clinical and Experimental Relevance

Understanding the fidelity and function of the **Off Response** is crucial in the study of visual disorders and for designing clinical diagnostic tools. Conditions affecting retinal function, such as glaucoma or various forms of inherited blindness, often show differential degradation in the On versus the Off pathways.

For example, some studies suggest that certain retinopathies might preferentially damage the inner retinal layers where On signals are processed, leaving the Off signals relatively intact, or vice versa. Electrophysiological tests, such as the electroretinogram (ERG), utilize specific stimulus protocols (e.g., flash stimuli administered on a dark background versus a light background) to isolate and measure the integrity of the Off pathway components (often reflected in the b-wave component of the ERG response). Anomalies in the off response magnitude or latency can serve as specific biomarkers for localized retinal damage or neurodegeneration.

Furthermore, contemporary research into retinal prosthetics often utilizes the principles of the off response. Effective artificial vision devices must not only stimulate cells that respond to light but must also accurately replicate the timing and intensity of the natural off response to provide useful information about contrast and movement, demonstrating the enduring importance of this basic neurophysiological concept.

Further Reading

[Depolarization \(Neuroscience\)](#)

[Visual System](#)

Receptive Field

Retinal Ganglion Cell

Glutamate in Neurotransmission

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