

Contrast Enhancement

Synonyms

Receptive field selectivity; Edge enhancement; Sharpening; Acutance; Unsharp masking; Selective feature enhancement; Decorrelation

Definition

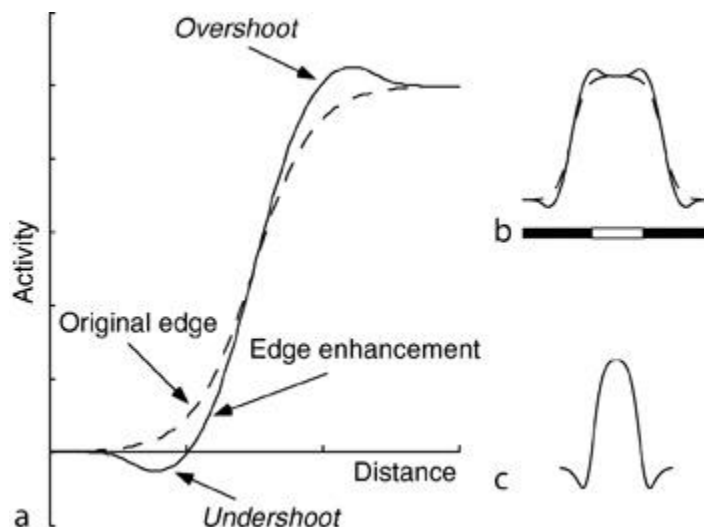
Contrast enhancement is a transformation of a sensory representation that results in an output representation in which regions of transition (e.g. "edges") are selectively emphasized. The mechanisms mediating contrast enhancement in different systems are diverse, depending critically on the breadth of the contrast enhancement function as well as on the modality of the representation.

Characteristics

Quantitative Description Across Modalities and Scales

The utility of contrast enhancement is broadly familiar from photography, particularly digital photography, in which it is employed to help compensate for the physical limitations of photographic equipment in comparison to the capacities of the human visual system. Indeed, several image processing techniques including contrast enhancement resemble stimulus-transformation processes embedded in animal sensory systems. Interestingly, the essential function of contrast enhancement is remarkably similar among sensory modalities (e.g. vision, audition, olfaction) as well as between these biological systems and photographic image processing, although the algorithms and neural mechanisms mediating this transformation differ substantially according to the differing constraints of these systems.

Contrast enhancement is a general term encompassing a range of related operations distinguished by scale (or breadth), which in this context refers to the maximum distance from any given point in an image or sensory representation at which local activity exerts an influence over the contrast enhancement operation. The simplest, smallest-scale contrast enhancement operation is edge enhancement (Figs. 1a-c).



Contrast Enhancement. Figure 1 Contrast enhancement functions. In all figures, the abscissa represents distance in the appropriate metric space (e.g. spatial location for visual retinotopy, frequency for audition, or odor similarity for olfaction), whereas the ordinate represents activity. (a) Edge enhancement. The original edge of the image or representation (dashed line) smoothly transitions from a low-activity (e.g. dark) region to a high-activity (e.g. bright) region. After edge enhancement (solid line), the acutance (maximum slope of the curve) has been increased. Additionally, both unsharp masking and lateral inhibition can produce regions of overshoot adjacent to the edge, which further emphasize the transition. This is the basis for the perception of Mach bands. (b) The "Mexican hat" function representing on-center/inhibitory surround contrast enhancement, here depicted in one dimension. Dashed line: activity profile induced by a stimulus (white bar) on a blank background (dark bar). Solid line: activity profile after edge enhancement. (c) Another form of the Mexican hat function in which the activated region is smaller than the scale of the contrast enhancement function and hence can be approximated by a point. Consequently, this form of the function does not exhibit prominent overshoots, though it does exhibit undershoots (surround inhibition).

Neighboring points in a sensory representation (or photographic image) that differ in intensity (e.g. brightness) are transformed so that these differences are accentuated. Specifically, local changes in intensity are emphasized by increasing acutance, the local derivative of intensity with respect to space. In digital photography, the most common algorithm for edge enhancement is the unsharp mask, whereas in the retina of the eye (for example) this transformation is instead mediated by lateral inhibitory synaptic interactions among neighboring neurons. Because both these operations utilize only information from immediately adjacent locations within the representation, they are considered to operate on the smallest relevant scale. At the other extreme of scale, in which the unsharp mask is uniform or, equivalently, lateral inhibitory interactions are uniform in strength and connect all possible pairs of neurons irrespective of distance, the resulting transformation is a global normalization roughly comparable to a z-score [1]. Winner-take-all and winner-take-most algorithms are potential variants of this global-scale contrast enhancement operation.

Contrast enhancement operations acting at intermediate scales are of considerable computational interest in neural systems. Potentially, they can address the global dynamic range problem created by sensory scenes in which different regions of potential interest exhibit substantially different mean intensities. Normally, in sensory scenes with distinct regions exhibiting widely different mean intensities, a simple optimization of the sensory system for the properties of one selected region renders it correspondingly poorly optimized for dissimilar regions. For example, setting a camera to capture the detail of a well-lit surface can result in the detail of darker regions within that photograph being lost. In digital image processing, local contrast enhancement, which operates on a scale between edge enhancement and global normalization, alleviates this problem by transforming images with respect to the intensity of a somewhat broader region surrounding each point. The underlying algorithm is typically a simple unsharp masking on a larger scale (i.e. greater blur distance) than is used for edge enhancement; however, superior results can be obtained by utilizing more complex, scene-dependent adaptive transfer functions integrating multiple independent samples. The analogous operations in biological sensory systems are topics of substantial interest and debate.

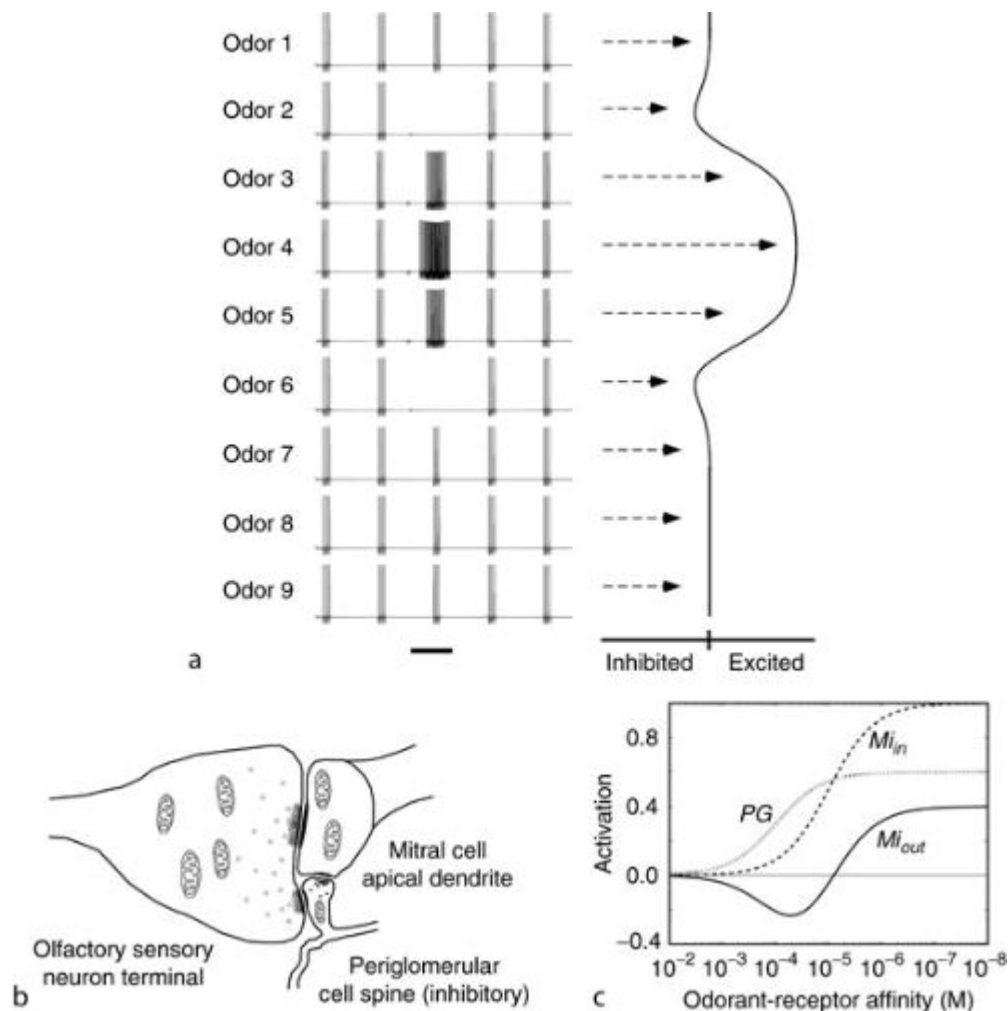
In each of these examples, an ordered topology among sensors is a necessary prerequisite for contrast enhancement computations. That is, the array of sensors must be somehow organized so that computations can be selectively performed among sensors with respect to the similarity (or degree of overlap) of their receptive fields. The degree of receptive field dissimilarity is referred to as distance - not necessarily based on physical space but rather on a distance

metric based on this ordered topology of stimulus similarity. For example, in digital image processing, creating an unsharp mask requires specification of the blur distance, which in turn requires a metric with which to compute distance and proximity in visual space. In the retina, physically neighboring visual neurons mediate correspondingly similar spatial receptive fields; hence, physical proximity naturally reflects receptive field similarity. In the auditory modality, the analogous similarity metric is frequency. While frequency is not an intrinsically spatial stimulus feature, the ordered distribution of frequency selectivity along the cochlea again enables the physical proximity of higher-order sensory neurons to reflect the similarity of their receptive fields. That is, these two neural systems are organized specifically so as to be able to utilize physical proximity to represent receptive field similarity, which renders effective the use of neural algorithms dependent on physical proximity, such as nearest-neighbor lateral inhibition. This solution is not effective in all modalities, however, as is discussed below.

Contrast enhancement is in essence a nonuniform rescaling of intensity information across a sensory scene that accentuates certain features of the sensory scene in exchange for a theoretical loss of absolute intensity information among those features. (This may result in little practical loss when the absolute range of intensities exceeds the instantaneous dynamic range of the sensory system). The scale of the contrast enhancement operation determines its function, which can range from edge enhancement at the smallest scales to global intensity normalization (e.g. exposure control) at the largest scale, with substantial potential at intermediate scales to contribute to selective feature extraction. While these definitions and principles are generally applicable, effective neural mechanisms for computing contrast enhancement operations depend critically on the properties and constraints of each sensory modality.

Olfactory Contrast Enhancement

Contrast enhancement operations are clearly evident within the olfactory system. Specifically, they are directly observable in the activity profiles of second-order principal sensory neurons, known as mitral cells, located within the olfactory bulb [2] (Fig. 2a).



Contrast Enhancement. Figure 2 Features of olfactory contrast enhancement. (a) Computational model of non-topographical contrast enhancement [3] replicating the canonical demonstration of olfactory contrast enhancement among olfactory bulb mitral cells [2]. Activity from a single mitral cell is illustrated over five inhalation cycles; the cell exhibits weak periodic background activity in response to inhalation of room air. One 2-second odor stimulus is delivered during the third inhalation cycle (denoted by black bar). Nine different odors are presented that vary sequentially in structural and perceptual similarity (odors 1-9, corresponding to a homologous series of *n*-aliphatic aldehydes in [2]). Here, odor 4 is near the center of this cell's receptive field, with its neighboring odorants also evoking activity and odors 2 and 6 evoking a net inhibition. This response profile reflects a Mexican hat contrast enhancement function, as illustrated to the right, based on a metric of odor similarity. (b) Illustration of the synaptic triad between OSN axonal terminals, mitral cell apical dendrites, and the spines of inhibitory periglomerular interneurons. OSN activity is communicated to the mitral cell both directly as excitation and via the periglomerular cell as inhibition. (c) Illustration of the central principle of non-topographical contrast enhancement [3]. The higher input resistance and smaller volume of periglomerular spines (PG) is proposed to generate a more sensitive voltage response to similar OSN inputs compared with mitral cell dendrites (Mi_{in}), but also to saturate at a level that the latter can overcome. The result is a nonmonotonic "half-hat" response profile of mitral cells to odorants of varying quality ($Mi_{out} = Mi_{in} - PG$), in which high-affinity odorants evoke excitation, medium-affinity odorants evoke inhibition, and low-affinity odorants evoke no response from mitral cells, yielding odor response profiles as shown in a. Further details in [1,3,4].

Odor stimuli evoke characteristic activity profiles across a broad range of different primary olfactory sensory neurons (OSNs); some OSNs become strongly activated by a given odorant while others are activated weakly or not at all. OSNs synapse directly onto mitral cell dendrites, as well as onto periglomerular cell spines which subsequently inhibit the same mitral cell dendrites (Fig. 2b). Consequently, mitral cell responses to odorants can be either predominantly excitatory or inhibitory, and have been shown to exhibit "Mexican hat" tuning curves for odor stimuli; i.e. odorants that are structurally and perceptually similar to those evoking peak activity in a given mitral cell evoke the strongest inhibitory responses from that cell (Figs. 1c and 2a). In other words, mitral cell response profiles exhibit "on-center, inhibitory surround" receptive

fields, in which the metric that defines this "surround" is based on chemical similarity rather than on physical space. This unique similarity metric necessitates an underlying neural mechanism quite different from those utilized by the visual and auditory systems.

Principles of Operation

Olfactory contrast enhancement and its underlying neural mechanisms exhibit important differences from their visual and auditory counterparts. First, of course, the similarity metric in olfaction is unique. In visual retinotopy, neuronal receptive fields naturally overlap in proportion to their spatial proximity; in audition, the cochleotopic mapping of auditory frequency selectivity accomplishes the same effect, enabling spatial proximity to be utilized as a proxy for receptive field similarity in subsequent neural computations. Consequently, nearest-neighbor lateral inhibitory synaptic interactions are able to mediate small-scale contrast enhancement in both these systems, though in audition the similarity metric is defined along the single dimension of frequency rather than the two-dimensional matrix of retinotopic space. The similarity metric in olfaction is somewhat more complex. Primary olfactory receptivity is mediated by ligand-receptor interactions between odorant molecules and a population of hundreds of different cell surface receptors expressed (in vertebrates) in ciliary membranes lining the olfactory epithelium within the nasal cavity. The different classes of olfactory receptor each respond to a range of structurally related molecular epitopes (odotopes; [4]), and the chemical receptive fields of different receptor classes overlap substantially, such that even single-molecule odorant stimuli can evoke activity in a substantial number of differently-tuned sensory neurons. Because of these broad receptive fields, structurally similar odorant molecules evoke correspondingly overlapping patterns of activity in the olfactory bulb and their odors are perceived as correspondingly similar in quality [5]. However, because of the number of receptor classes, the similarity metric is also high-dimensional (in principle, the number of dimensions should correspond to the number of different odorant receptors expressed; [4]). Consequently, a distance matrix of odorant similarities, whether defined perceptually or in terms of neuronal activation profiles, cannot be continuously mapped onto a one- or two-dimensional surface as can the cochleotopic or retinotopic maps of the auditory and visual modalities. Rather, such metric spaces must be mapped discontinuously when mapped onto lower-dimensional spaces such as the two-dimensional cortical layer of the olfactory bulb, thereby exhibiting exactly the sort of fragmented topology exhibited in the glomerular layer of the olfactory bulb. Nearest-neighbor lateral inhibition is therefore ruled out as a possible underlying neural mechanism for olfactory contrast enhancement.

Olfactory contrast enhancement entails sharpening mitral cell receptive fields so that the population activated by a given odorant is more specific and the overlap between the representations of similar odorants is correspondingly reduced. That is, an operation must be performed that is analogous to lateral inhibition, but that is effective in a high-dimensional metric space. A non-topographical mechanism for olfactory contrast enhancement has been proposed that is independent of the proximity among activated neurons, combining a small-scale contrast enhancement mechanism with a qualitatively distinct global-scale mechanism mediating feedback normalization among activated mitral cells [1,3]. While the mechanisms are unrelated, the resulting transformation is comparable to that which would be mediated by a "lateral" inhibitory mechanism mapped directly onto the high-dimensional topology of similarity among OSN receptive fields.

Regulation of Olfactory Contrast Enhancement

Many factors - behavioral, situational, pharmacological, and genetic - affect the perceptual differentiation among similar odorants that is influenced by contrast enhancement. The clearest correspondence to date between such perceptual differentiation and the regulation of contrast enhancement at the neural circuit level, however, is the neuromodulation of olfactory bulb circuitry by acetylcholine. Nicotinic cholinergic agonists excite both mitral and periglomerular neurons in the olfactory bulb [6], yielding a concerted response predicted by the non-topographical contrast enhancement model to sharpen mitral cell tuning curves. Indeed, infusion of cholinergic agonists into the olfactory bulb evokes sharper behavioral differentiation among odorants [7]. The implication of this example is that olfactory contrast enhancement is plastic, with differentiation among odor representations dynamically regulated in accordance with variables such as learning, motivation and behavioral state.

Contrast Enhancement and Olfactory Function

The function of contrast enhancement in any system is to differentially emphasize particular features within a sensory scene. Traditionally, this process of feature selection is discussed with reference to the physical attributes of sensory scenes: e.g. visual edges, or the relative differentiation among structurally similar odorant stimuli; however, this is not a

requirement. Feature selectivity filters at any level comprise essentially the same operations as are here termed contrast enhancement. Of particular interest in the olfactory system are the potential contrast enhancement capabilities of the external plexiform layer - a deeper layer of the olfactory bulb in which mitral cell secondary dendrites interact reciprocally with inhibitory granule cells and hence indirectly with each other. That is, this layer mediates lateral inhibition among mitral cells, though the pattern of this inhibition does not appear to reflect a two-dimensional center-surround architecture [8,9]. While it has been argued that this processing layer lacks the full complement of afferent information necessary to mediate contrast enhancement with respect to physical stimulus attributes [3,4], it appears architecturally capable of manipulating high-dimensional stimulus representations, and hence of mediating feature-selective operations on odor representations using arbitrary scales and masks that are not constrained by the externally-defined odotope similarity metric. For example, these masks may reflect prior odor experience and olfactory learning and could contribute to complex processing such as the binding of multiple structurally-unrelated odorant features into unitary odor percepts. However, while the circuitry and synaptic interactions within this layer are clearly plastic and responsive to odor learning [10], the function of this post-glomerular circuitry remains unclear.

Contrast enhancement is a general term for what might in retrospect be more broadly referred to as selective feature enhancement, and is a ubiquitous process in sensory systems. While the operational principles are common across sensory modalities, the basic properties of the olfactory modality necessitate underlying mechanisms for contrast enhancement that are dissimilar from those operating in other sensory systems. Neuromodulatory regulation of receptive field stringency in second-order olfactory principal neurons, and the plasticity of bulbar circuitry in response to olfactory discrimination learning, identify these contrast enhancement mechanisms as a crucial part of the adaptive plasticity of an active sensory system.

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