

effects demonstrate that the maturational state of the learner's brain is crucial for the attainment of a language system.

Several questions remain open about the mechanisms underlying language learning. One issue is whether specific aspects of language acquisition should be attributed to language-specific versus general-purpose learning mechanisms. Another issue is whether children's native language can affect the way they think, and whether language is necessary or helpful for the development of human concepts.

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*See also* Aphasias; Audition: Cognitive Influences; Context Effects in Perception; Speech Perception; Top-Down and Bottom-Up Processing; Word Recognition

### Further Readings

- Baker, M. (2001). *The atoms of language*. Oxford, UK: Oxford University Press.
- Bloom, P. (Ed.). (1993). *Language acquisition: Core readings*. Cambridge: MIT Press.
- Chomsky, N. (1986). *Knowledge of language: Its nature, origin, and use*. New York: Praeger.
- Clifton, C., Frazier, L., & Rayner, K. (Eds.). (1994). *Perspectives in sentence processing*. Hillsdale, NJ: Lawrence Erlbaum.
- Gleitman, L., & Liberman, M. (Eds.). (1995). *An invitation to cognitive science: Vol. 1. Language*. Cambridge: MIT Press.
- Pinker, S. (1995). *The language instinct*. London: Penguin Books.
- Trueswell, J., & Tanenhaus, M. (Eds.). (2006). *Approaches to studying world-situated language use*. Cambridge: MIT Press.

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## LATERAL INHIBITION

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*Lateral inhibition*, is a decrease in response in neurons that occurs when neighboring neurons become activated. For example, in Figure 1(a), a network of 10 excitatory neurons receiving information from visual space (such as neurons in the retina or later levels of the visual system) is intermingled with 9 inhibitory neurons. Activity in any one of the excitatory neurons can inhibit its neighbors indirectly by activating the inhibitory

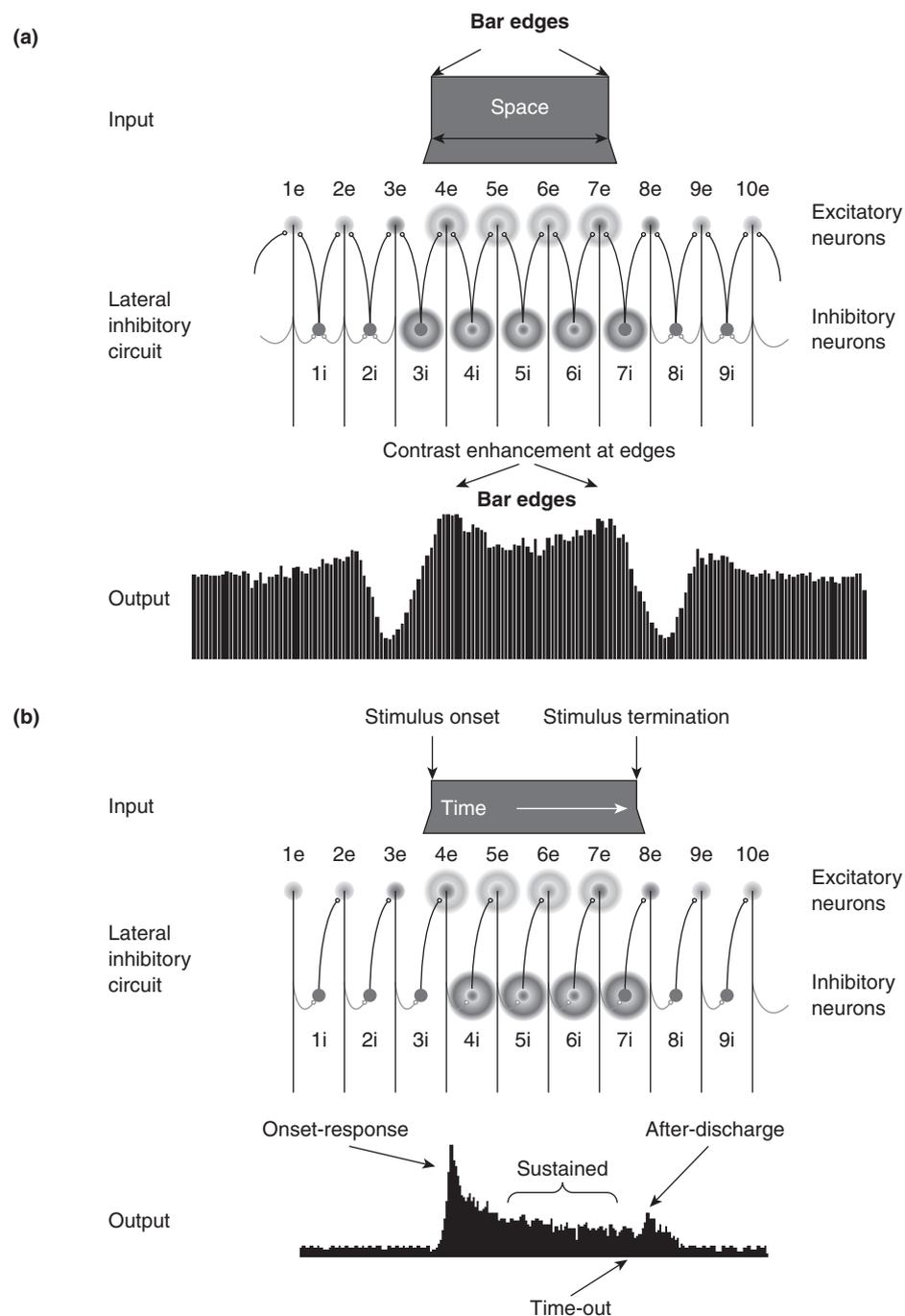
neurons that then inhibit their neighbors. When a stimulus (such as a bar of light or any other stimulus) excites a number of neurons in the network (in this case neurons 4e, 5e, 6e, and 7e), the effect of inhibition is to suppress the neurons just outside the edge of the bar (3e and 8e) because those neurons are inhibited but not excited. Further, because the neurons just inside the edges of the bar (4e and 7e) are excited by light and only inhibited by one neighbor, they are especially active. This leads to perceptual contrast enhancement at borders. Further research showed that lateral inhibition also applied to overlapping stimuli, and that its strength fell off with distance between the interacting stimuli.

Haldan Keffer Hartline won the Nobel Prize in 1967 for discovering lateral inhibition and its neural correlates. The first inhibitory circuit in the nervous system was found in the horseshoe crab (*Limulus polyphemus*). Here, an activated photoreceptor was inhibited when a laterally adjacent (or nearby) photoreceptor was also activated. Lateral inhibitory circuits are currently known to be ubiquitous to all sensory areas of the brain, and they play an important role in many sensory, cognitive, motor, affective, and limbic processes. The most common mechanism by which neurons suppress their neighbors is through the inhibitory neurotransmitter gamma-aminobutyric acid (GABA).

Hartline and his collaborator, Floyd Ratliff, went on to characterize the three components of a laterally inhibitory circuit: (1) Excitatory input and output—information input arrives at a given sensory area of the brain in the form of excitatory neural responses. Information output is sent to the next area(s) in the hierarchy also in the form of excitatory neural responses; (2) Self-inhibition—neurons that laterally inhibit their neighbors also inhibit themselves; (3) Lateral inhibition occurs as a function of excitatory activation—thus inhibition follows excitation in time.

### The Role of Lateral Inhibition Through Time

In addition to its effects across space, lateral inhibition also leads to temporal effects over time. Let us now examine two neurons embedded within a lateral inhibitory network as a function of time (Figure 1b): one excitatory neuron (at times 1e



**Figure 1** Spatial Lateral Inhibition Model

Notes: (a) A mammalian representation of the spatial lateral inhibition model originally proposed by Hartline and Ratliff. The excitatory neurons in the center of the upper row receive excitatory input from a visual stimulus. This excitation is transmitted laterally to the inhibitory neurons just outside the stimulus and within the area impinged on by the stimulus. The inhibitory interactions between excited neurons at the edges of stimuli and their non-excited neighbors results in apparent contrast enhancement at the borders of the stimulus. Output of each of the excitatory neurons is represented in action potentials per unit time at the bottom. (b) One excitatory and one inhibitory neuron taken from the spatial model in (a), now followed through a period of time in which the stimulus is off (times 1, 2, and 3), on (times 4, 5, 6, and 7), and then off (times 8, 9 and 10).

through 10e) and its connected inhibitory neuron (at times 1i through 9i). At times 1e, 2e, and 3e (before the stimulus is presented), there is no excitatory input, so the output remains flat. At time 4e (just after the stimulus, such as a bar of light, is presented), the neuron is excited, causing an onset-response. This leads to the activation of the inhibitory neuron at time 4i, after a slight delay. The inhibitory neuron then feeds back on the excitatory neuron and causes its activity to be suppressed at time 5e. This state of excitatory-inhibitory equilibrium is called the sustained period, which continues through time 7e, after which the stimulus is extinguished. Despite the stimulus having been terminated, the neuron at time 7i is nevertheless activated by the excitatory neuron at time 7e because of the delayed effect of inhibition. Thus, the excitatory neuron at time 8e is inhibited while not being excited by visual input, and so is in a state of deep suppression called the time-out period, which in turn causes the inhibitory neuron at time 8i to be deeply suppressed because of lack of input. The excitatory neuron at time 9e then exhibits a disinhibitory rebound called the after-discharge because of the lack of baseline inhibition (even though there is no excitatory input).

Therefore, just as lateral inhibition causes neurons to respond strongly to spatial borders of stimuli, it also makes them respond strongly to temporal borders (the onsets and terminations) of stimuli. The perceptual result of this is contrast enhancement at the temporal borders of stimuli.

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*See also* Contrast Enhancement at Borders; Vision: Temporal Factors; Visual Illusions

### Further Readings

- Hartline, H. K. (1939). Excitation and inhibition of the “off” response in the vertebrate optic nerve fibers. *American Journal of Physiology*, 126, 527.
- Macknik, S. L., & Livingstone, M. S. (1998). Neuronal correlates of visibility and invisibility in the primate visual system. *Nature Neuroscience*, 1(2), 144–149.
- Macknik, S. L., & Martinez-Conde, S. (2004). The spatial and temporal effects of lateral inhibitory networks and their relevance to the visibility of

spatiotemporal edges. *Neurocomputing*, 58–60C, 775–782.

Ratliff, F. (1965). *MACH BANDS: Quantitative studies on neural networks in the retina*. San Francisco: Holden-Day.

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## LAZY EYE

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*See* Amblyopia

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## LIGHT MEASUREMENT

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Light provides humans with stereoscopic images of the world at all distances. This entry considers measuring light as it affects human vision. Humans are most sensitive to electromagnetic radiation in a small window between 400 and 700 nanometer (nm) wavelengths ( $\lambda$ ). This response begins with four types of retinal receptors. After sitting in a light-free room for an hour, humans report seeing light with only four to six photons. Snow on a mountaintop sends to the eye 100 million times more photons. Although photographic film has a fixed, unique response to the number of photons/area, human visual appearance has a complex spatial relationship to the light on the retina. Nevertheless, light measurement in psychophysics is important: first, to accurately describe the display presented to observers, so others can reproduce the experiment; and second, to describe the light array, pixel (picture element) by pixel, of the entire field of view, as input for computer appearance models.

### Radiometry

Radiometry, a part of physics, describes standards for measuring electromagnetic radiation. Photons with different wavelengths have different energies. From Planck’s law, we can calculate that a single 555-nm photon’s energy equals  $3.6 \times 10^{-19}$  joules (or, watt  $\times$  seconds).

*Irradiance* is the measure of the energy from the number of photons continuously falling on an area. Irradiance meters measure (watts/centimeter [cm]<sup>2</sup>)