

CHAPTER 6

PRINCIPLES OF NEURAL CIRCUITS.

6.1. CONNECTIONS AMONG NEURONS

Neurons are interconnected with one another to form circuits, much as electronic components are wired together to form a functional circuit. Many neural circuits together form a neural system, just as many electronic circuits together form a device such as a computer or a TV. The connections in neural circuits can be classified into a few basic patterns:

Divergence.

Output from one neuron onto many. Each postsynaptic neuron receives input from the same presynaptic neuron, but may react to it differently.

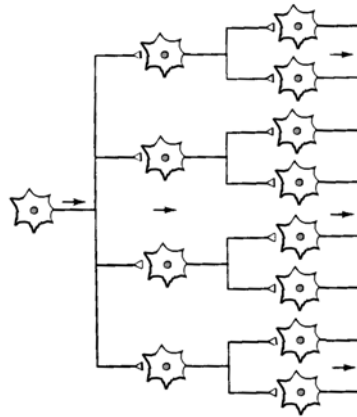


Figure 6-1. In a divergent neural circuit, the axon of one neuron branches to send information to multiple target neurons. Divergent output allows the same signal to reach many different neurons.

Convergence.

Output from many neurons onto one. Many different presynaptic neurons provide input to a single postsynaptic neuron. These inputs may be excitatory or inhibitory, and may be active at different times.

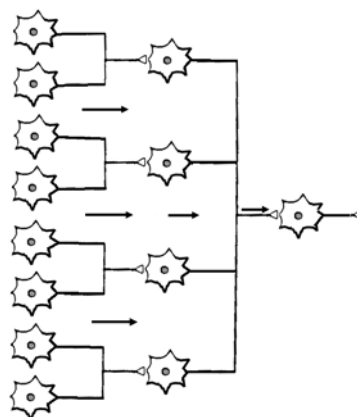


Figure 6-2. In a convergent neural circuit, the axons of multiple neurons all send information to a single target neuron. Convergent output allows different signals to reach one neuron for comparison or integration.

Feedback.

Output is from the postsynaptic neuron back onto one or more neurons presynaptic to it. A neuron may even send an axon branch back onto itself.

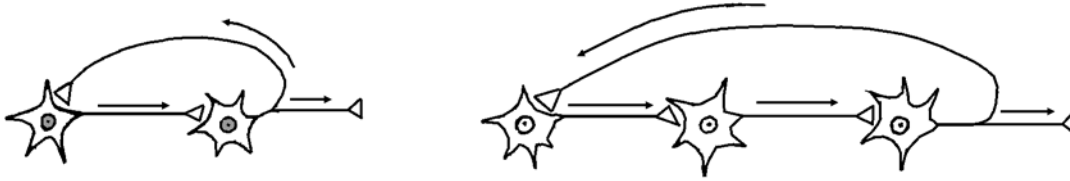


Figure 6-3. In a feedback circuit, a neuron projects back to one that had already provided direct (left) or indirect (right) input to it.

6.2. REPRESENTATION OF INFORMATION IN NEURAL CIRCUITS

Neural circuits are usually thought of as representing information in the form of a pattern of action potentials, since this is the means by which information is transmitted from one point to the next in the nervous system. A neural representation of information is often referred to as a "*neural code*".

We can also think of information as being represented by graded potentials at the level of single neurons, since the graded potential reflects the information content of the input(s) to the neuron.

6.2.1. Models of neural "coding".

Information may be represented in terms of which neurons are active over a given time period, and/or by the distribution of action potentials in these neurons over time. Thus, the basic models of neural coding are:

Spatial codes.

In a spatial code, or *place code*, the relevant information is which neuron(s) are active at a given point in time, or over a particular time period. There are two main models of spatial codes:

- *Labeled lines.* In a labeled line representation, activity in any individual neuron unambiguously signals a particular stimulus attribute and is independent of the amount of activity in other neurons. The rate of firing (or total number of spikes fired over a specific time period following a stimulus) is commonly assumed to convey information about stimulus strength.

- *Population code.* In a population code, the important information is the relative amounts of activity in different members of a population of neurons, not the absolute amounts of activity. The level of activity in any single neuron cannot convey unambiguous information about the stimulus, but depends on context.

Temporal codes.

In a temporal code, information is represented by the distribution of action potentials over time. In actuality, information is usually represented in the nervous system by a combination of spatial and temporal coding, resulting in a *spatiotemporal code*. This means that the relevant information is conveyed by which neurons are active, and when each is neuron is active.

6.3. PROCESSING OF INFORMATION IN NEURAL CIRCUITS.

Neurons in circuits process information by combining and *integrating* information from different sources. This is done through interaction of EPSPs and IPSPs at the level of single neurons. Integration may take various forms, but can best be thought of as a process of *algebraic summation*. Integration can be thought of as occurring over both space and time.

Spatial summation

Spatial summation occurs when an individual neuron receives simultaneous inputs from multiple sources. The small EPSPs contributed by many different synaptic terminals add up to produce a single large EPSP that may be sufficiently large to reach threshold. Similarly, many small IPSPs may add up to produce a large IPSP. EPSPs and IPSPs from different sources may cancel each other out so that the result is the net sum of both, or even zero.

Temporal summation

Temporal summation occurs due to the fact that every postsynaptic potential has a finite time-course, usually lasting at least several milliseconds. This means that if a second input arrives before the EPSP or IPSP elicited by the previous one has finished, the two can add together (algebraically, of course).

Thought question: What different types of information processing could be performed by a system in which different units (neurons) are sensitive to slightly different ranges of a stimulus parameter (e.g., pitch of a sound, visual space) and there is divergence, convergence, excitation, inhibition, spatial summation and temporal summation?

6.4. FORMATION AND MODIFICATION OF NEURAL CIRCUITS.

Neural circuits are first formed during development through processes that are largely beyond the scope of this course. Briefly, though, neural development depends in part on genetic makeup, partly on the internal and external environment, and partly on experience. Although all brains are similar, no two are exactly alike, not even those of identical twins.

Humans are born with most of the same neurons that they will keep throughout their entire life. If neurons die, they are generally not replaced. With few exceptions, once you lose neurons, they are gone!

Synaptic connections, however, *can* and do change. As you grow, mature, learn, and experience the world your brain is continually forming new connections (and possibly breaking

old ones). It is this plasticity that allows you to learn new skills, adapt to new conditions, and change old habits. During this process, the axons and dendrites of neurons can grow and branch, or retract and reform elsewhere. In addition to forming new synapses, existing synapses can be strengthened or weakened. When you learn, your brain changes. You do not usually grow more neurons, but the ones you have rearrange themselves.

Thought question: Adult mammals, including humans, have lost most of their capacity to generate new neurons. What are the (obvious) disadvantages of this evolutionary adaptation? What are the advantages? Why might the advantages outweigh the disadvantages?

6.5. GENERAL PRINCIPLES OF SENSORY INFORMATION PROCESSING

Modality Specificity.

At least initially, each sensory system has its own separate pathway. For example, information transmitted from the eye via the optic nerve remains completely separate from information transmitted from the ear via the auditory nerve. We perceive the input from the optic nerve as “sight” and that from the auditory nerve as “hearing” simply because that is how we have learned through experience to interpret information from these two sources.

Filtering.

Within each sensory modality, different receptor cells and/or nerve fibers are maximally sensitive to and activated by a specific set of stimulus conditions. For example, because of the mechanical properties of the ear, different auditory receptor cells and auditory nerve fibers respond best to different frequencies (pitches) of sound. Because of the different light-absorbing properties of receptor cells in the eye, different receptors respond best to different wavelengths of light, corresponding to different colors. Because receptors are distributed in a sheet across the back of the eye, different receptors respond to light originating in different places in the visual field.

Tuning.

The filtering process results in cells that respond best to stimuli with specific properties, i.e., a specific range of values along a measurement scale corresponding to one stimulus variable. For example, a given auditory nerve fiber responds to some degree over a certain range of frequencies, and there is one frequency that elicits the largest response. Different fibers are tuned to different frequency ranges. One fiber might respond to frequencies between 200-500 Hertz (Hz; cycles/second) with a response maximum at 350 Hz and another to 600-800 Hz with a maximum at 700 Hz.

Similarly, one visual receptor cell might respond over a range of wavelengths from 400-600 nanometers (nm), with the best response at 500 nm. There would be other receptor cells tuned to different ranges of wavelengths, with response peaks at different values.

Formation of spatial representations (topographic maps).

Receptor cells in many sensory systems are distributed spatially in an organized array. In such an array of receptors, different ones have different filter properties and tuning. Often there is a systematic organization of cells tuned to different values of a stimulus parameter. In the

auditory system, for example, the receptors are arranged in such a way that frequency tuning progresses from high frequencies at one end to low frequencies at the other. In the eye, the arrangement of receptors on the retina corresponds to position in the visual field. As a result, the receptor array contains a topographic representation or “map” of sound frequency, visual space; or other stimulus dimension.

Generation of temporal patterns.

Sensory stimuli are distributed in time, and receptors and nerve fibers are active at times that are correlated with the temporal pattern of the stimulus. For example, an auditory nerve fiber responds each time there is a tone, but does not respond during the times between tones. The temporal pattern of neural activity therefore directly reflects the temporal patterning of the stimulus.

Integration within a modality: Integration across “space”

Because different receptors (and ultimately neurons) have different tuning and filtering properties, a complex sensory stimulus will cause activity in multiple receptors (or neurons) corresponding to multiple “channels”. Information processed in different channels has to somehow be combined to produce the “big picture”. For example, information from different points in the visual field has to be combined in order to perceive an object, and information from different auditory nerve fibers must be integrated to perceive a musical chord or a person’s voice.

Integration within a modality: Integration across time.

To understand the dynamic nature of the sensory world, information present at one time has to be related to and linked with information that is present earlier and later. For example, the sequential stimulation of multiple visual receptors, corresponding to different points in the visual field results in perceived movement. Sequential stimulation of multiple auditory nerve fibers might result in the perception of a melody.

Integration across modalities.

In many cases an object or occurrence in the environment will stimulate more than one modality. In order to get full and accurate information, information from one modality must be compared with information from other modalities. For example, we often correlate what we see with what we hear. The temporal pattern of changes in the lip movements of a speaker aids in perception of the words that are heard. Sounds coming from a loudspeaker are typically localized to the person perceived to be producing the sounds rather than from the loudspeaker itself, which may be in a very different place.

Interaction between sensory and motor systems.

Often sensory stimuli lead to motor responses. These may take a number of forms:

Reflex responses occur rapidly, without conscious thought, through a short pathway. Withdrawal of one’s hand from a hot stove is a good example of a reflex that occurs in the spinal cord.

Volitional responses are responses that occur after conscious thought. They take longer, and presumably require cortical processing. An example would be turning off the stove when the food you are cooking is done.

Learned Responses may be volitional at first, and reflex later. A skilled pianist, dancer, or skier is not conscious of all movements being made, even though these same movements were executed consciously while learning the skill.

Sensing of motor action and motor feedback on sensory systems is important for smooth and accurate motor performance. For example, muscles, joints and tendons have sensory receptors that monitor stretch, contraction, position, etc. and provide constant updates to the brain. Sensory systems provide information about the relation of the body to its surroundings. Comparing these two forms of information allows us to interact with the environment.

Learning and memory formation.

Not all sensory input results in motor actions. Much information is simply “stored” for future reference. Even when motor action does occur, comparison of sensory input in one modality (e.g., vision) when compared with input from another modality (e.g., touch) can result in memories that lead to adjustment of the relation between the two modalities. This happens extensively during postnatal development. Information about seeing objects and reaching for them results in an internal (brain) representation of space in which visual space is in register with somatosensory space.

Synthesis of information and creativity.

Our sensory systems take in information about the world, and much of this information is “stored”. However, our brains not only have the capacity to retrieve this information, but to transform it, recombine items of information in novel ways, and even create new sensory stimuli that we have never before perceived in the real world.