In:
What is Truth in Philosophy and in Different Scientific Disciplines
Eds. H. Hisaki and J. Niżnik, Wiedeń, pp. 11-20.

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What does the brain see?[1]

The new approach in physiology posits that the function of the brain's sensory systems is not to form a thorough representation of reality, but rather to start a fast and appropriate reaction to reality's changes. With such an approach, the sensory inputs are thought of not as donors of information – like in classic theories – but rather as catalysts of internal brain activity. The external stimuli are thus represented in the neural network by the impact they have on the functional state of the whole brain. Indeed, from original work conducted by Libet (1985) we know that conscious experience is built up much too slowly to control most of our behavior. The role of sensory perception is probably to control the overall strategic behavioral goal of the organism.

Many physiological properties of the visual system, the most researched sensory system in the human brain, provide strong support for the above hypothesis. The neuronal network of the brain consists of 10^{11} neurons of two kinds – excitatory and inhibitory. A simplified understanding of the information processing in the brain is that it relies on the addition and subtraction of activation of thousands and millions of single neurons in the network. See Figure 1: the activation of each of the three neurons is represented by the number of electrical impulses fired by each of them in the same unit of time, say, a second. The activity of inhibitory (–) and excitatory (+) neurons is transmitted via their output processes (axons) to the receiving processes (dendrites) of the summing neuron (=) and sets its frequency of firing to as many impulses per second as results from the simple arithmetic of the input it received. This straightforward rule allows us to understand the concept of the

[1] I thank Aleksander Sobolewski for his critical reading of the manuscript and Joanna Smyda for help in preparing the figures.

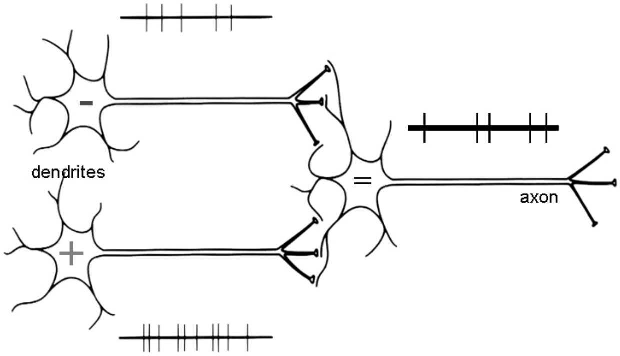

Figure 1. The calculations within the neural networks. Two neurons excite (+) or inhibit (−) the summing neuron (=) via one-way connections between processes arising from their cell bodies: receiving dendrites (many short and thin processes projecting from the cell's body) and output axons (one thick, branching out, process per cell). Electrophysiological recordings show one second long traces of voltage changes within each of the cells. The number of impulses (short-circuits of the voltage across the cell membrane) is proportional to the temporary excitation level of the cell.

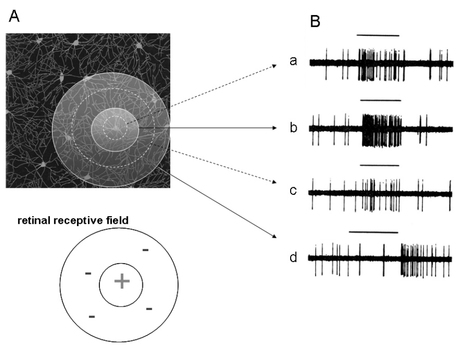

Figure 2. The receptive field of a retinal cell with the body located at the center of concentric circles in A. The dendrites of this cell extend outwards and cover an area around it encompassed by the inner solid circle. The surrounding cells' dendrites cover the neighboring areas. The recordings in B show the excitation of this cell evoked by stimulating it with a spots of light of different diameters shown in A. The strongest response of the cell is evoked by the spot covering the retinal area which includes all the receptors transmitting their excitation to the cell dendrites (b). The two largest spots (c, d) additionally encompass the area covered by the surrounding cells which exert the lateral inhibitory influences on the recorded cell. The duration of the light stimulus is marked above each recording in B (adapted from Hubel and Wiesel 1961).

receptive field – the part of retina which, when stimulated by light (or dark) spots, changes the firing frequency of a particular retinal cell. Figure 2A shows a network of retinal neurons with their receiving dendrites. In the example shown in Fig. 2A, the center of the retinal receptive field of one neuron (that in the innermost circle), that is the area containing retinal light receptors from which this neuron receives excitatory input, is the inner solid line circle. Therefore, when this area is illuminated by a light spot of a corresponding diameter, this neuron fires the greatest number of impulses per second (Fig. 2Bb). A spot of a smaller diameter, represented by the innermost broken line circle in Fig. 2A, illuminates a smaller number of receptors and the retinal cell fires less impulses (Fig. 2Ba). On the other hand, larger spots (the two outermost of the concentric circles in Fig. 2A) illuminate all of the central receptors, but also the receptors providing excitatory input to the dendrites of other surrounding retinal cells. This leads to a different summing result. All neighboring neurons in the neural net exert reciprocal, inhibitory action on each other – another general processing rule which is called lateral inhibition. Indeed, such an inhibitory influence results in a lower activation of neighboring cells when they are stimulated simultaneously. Returning to our example retinal neuron, if receptive field centers of surrounding retinal cells are also activated when a sufficiently large spot is flashed, they lower the firing frequency of our example neuron by means of lateral inhibition. (Note, that the surrounding neurons are also reciprocally inhibited by each other and by our example neuron). It follows that a light spot of a diameter equal to the receptive field center excites a single retinal neuron to the greatest degree. This area is therefore the smallest pixel which limits the spatial resolution of vision and the visual scene encompassed by the retina is divided into a matrix of about one million such pixels. The activity of this population is sent along the one million fibers of the visual nerve of the eye (and another million for the other eye) to higher levels of the visual system, where it is further integrated according to similar rules (see below).

Note, however, that already at the retina the simple mechanism of lateral inhibition modifies the incoming visual information. Of the one million retinal neurons, Fig. 3A presents the functional relations between some six aligned cells. A light edge is flashed across this row of cells so that it excites (+) the three leftmost cells, and the three rightmost cells are in the dark, not excited by the stimulus (0). The excited neurons inhibit laterally their closest neighbors (-). This means that the neuron at the edge of the lit area receives less inhibition than the other excited neurons. Conversely, the neuron at the edge of darkness is the only unexcited neuron to be inhibited. (Try "summing up" the pluses, zeros and minuses for each cell). The result of this "neuronal arithmetic" is sent along visual nerve axons further into the brain causing the illusion called the "Mach band"' (Fig. 3B, C). The simple summation

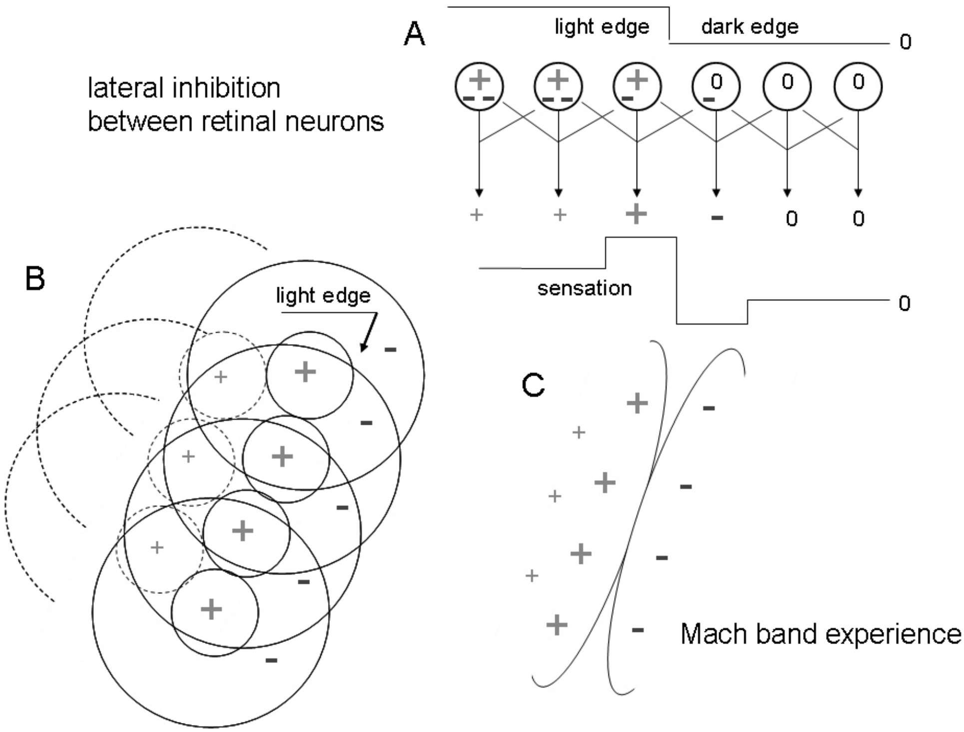

Figure 3. The Mach band – an illusory enhancement of edge contrast that is a result of computation in a network with lateral inhibition.

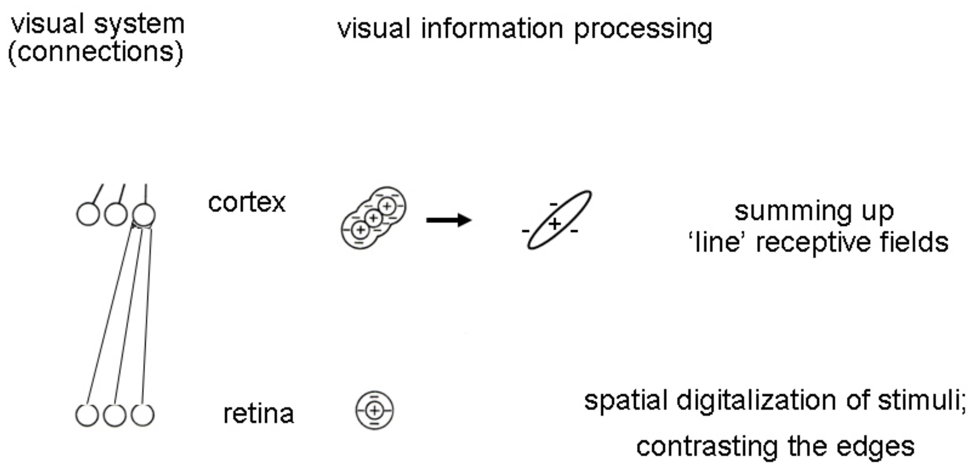

Figure 4. First order cortical integration of visual information results in a 'short line' receptive field of a specific orientation. The strongest activation of a cortical cell is evoked by a light bar of this orientation, which initially excites three aligned retinal input neurons.

of excitation and inhibition within the network results in enhanced sensation of contrast at the edges of the light and dark areas. It follows that even the information leaving the retina is already transformed by the neuronal network and does not represent the "truth" about the visual world.

When the information about the visual scene, split into pixels and partially elaborated by the retinal network, reaches the cortex it is integrated by cortical cells according to similar simple rules. Figure 4 provides an example of a single, first order cortical cell which receives convergent input from three aligned retinal "pixels". The summation of such input results in the receptive field of the cortical neuron being a "short straight line" of a specific orientation and position in the visual field. It follows that the stimulus which mostly activates such a neuron is a bar of light of the size and orientation fitting the excitatory part of the neuron's receptive field. The activation of this cortical neuron is the brain "seeing" a light line in a given part of the visual field and provides an element for building up networks representing more complicated stimuli (compare Fig. 7).

Imagine a neuron located in a second order visual cortical area which receives information from the first order cortical cell with the "short line" receptive field

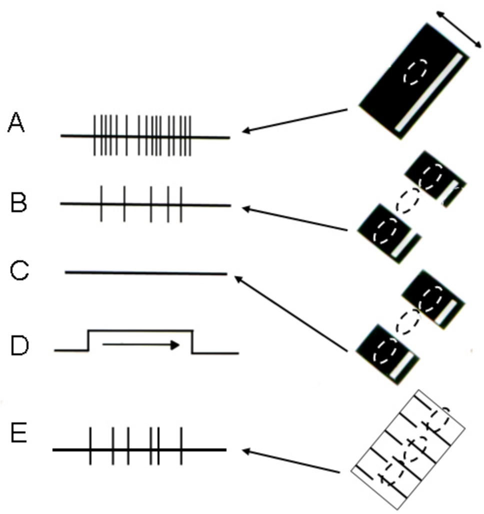

Figure 5. The neurons in a second order visual cortex are activated not only by an appropriate stimulus moving across its receptive field (A, D) but also, via the network of the neurons from a larger assembly, by same-orientation stimuli bars extending outside its classic receptive field (B). Where the two light bars are clearly separated, precluding the illusion of continuity, there is no activation of the assembly and no firing of the recorded cell (C). E, The illusory contour of an edge of appropriate orientation activates the assembly of neurons and the recorded cell which belongs to it. Adapted from van der Heydt et al. (1984).

(Fig. 5A), but having an additional activation input from network connections built up during visual experience by mechanisms of developmental plasticity (see below). This neuron was found to be activated by a bar of light of oblique orientation moving through its receptive field (the broken outline in the figure). This activation is reflected by the high frequency of firing as the light bar passes across the receptive field. Note, however, Figure 5B. Now, the stimulus is two light bars of similar orientation but moving beyond the neuron's classic receptive field. Although there is no direct stimulation of the receptive field the neuron also fires. This is not so in Fig. 5C, where the two light bars are clearly separated, precluding the illusion of continuity. These complex responses might be explained by the activity of the other cortical neurons with receptive fields positioned further away, at the extension of the "short line" receptive field of the recorded neuron. Such neurons with receptive fields of similar orientation are frequently activated together since many natural stimuli have continuous outlines. During the process of maturation of the visual system, groups of cells, which are frequently activated together, form strong mutual connections (compare Fig. 7). Such groups, called neuronal assemblies, are rapidly activated in their entirety if just some of their elements are excited allowing for clearing up of the visual noise. In the example shown in Fig. 5B, two neurons with their receptive fields flanking the recorded cell provoke its activation when the assembly they all belong to is activated by the stimulus shape (in this case, the line of the same, oblique orientation as shown in Fig. 5B, E) via inter-assembly connections. Cortical neurons may thus respond to stimuli which do not activate directly the receptors within their receptive fields. This rule leads to many illusory perceptions like those presented in Fig. 6. The implied white triangle (Fig. 6A) or the curved edge between similar textures (Fig. 5E and Fig. 6B) might be more informative for the brain than the actual pattern printed on the page. (Imagine, for example, that Fig. 6B is a glimpse of a tiger walking through tall grass!). This is why neuronal firing often represents "non-existent" stimuli, "con-

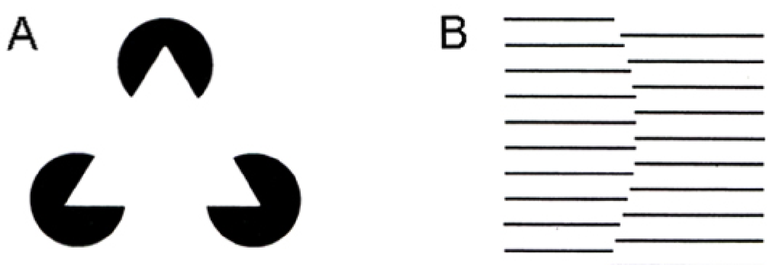

Figure 6. A, B. Illusory contours appear as a result of the temporary integration of a group of neurons forming a functional assembly.

structed" by automatically activated network connections, and not actual patterns in the visual scene.

A model of two assemblies embedded in a cortical network of neurons is shown in Fig. 7. The assembly marked by black dots is formed temporarily within the network by the simultaneous activation of three first order cortical neurons (also marked black). The activation of this assembly follows the appearance of a triangle (pointing up) in a particular location in the visual field (actual stimulus) and

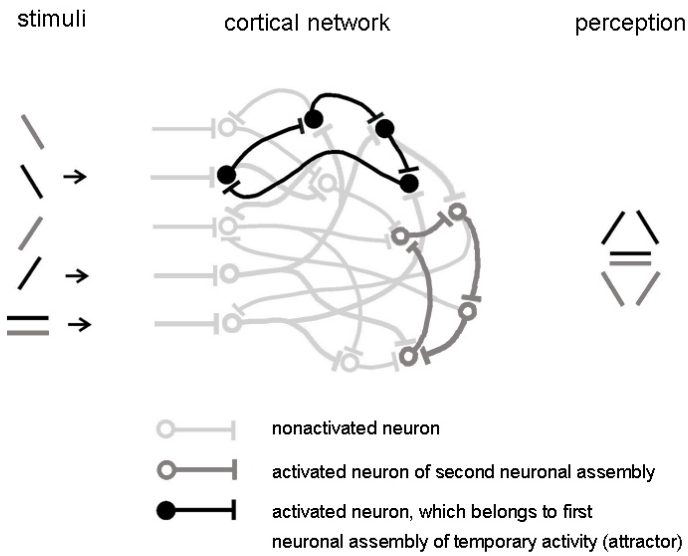

Figure 7. A model explaining the formation of an attractor for a specific stimulus – a group of neurons with inter-connections strengthened by frequent simultaneous excitation by that stimulus. See text for details.

represents an appropriate perception. The second assembly, representing a triangle pointing down, might be activated by a different set of input cells and could encompass a different group of neurons (marked by dark gray dots). Note, however, that the two groups of neurons (the two assemblies) bound by different functional connections could also include some of the same cells. This possibility of binding different functional network groups using the same elements greatly decreases the number of neurons needed for encoding the endless variety of stimuli which should be stored in the brain during a lifespan, and thus increases the capacity of its memory. The described model may also explain why the same visual pattern might be perceived differently at two consecutive moments. For example, in Fig. 8 either of the two three-dimensional structures can be perceived, but not at the same time. Accordingly, a small reorganization of the cortical activity pattern may remarkably

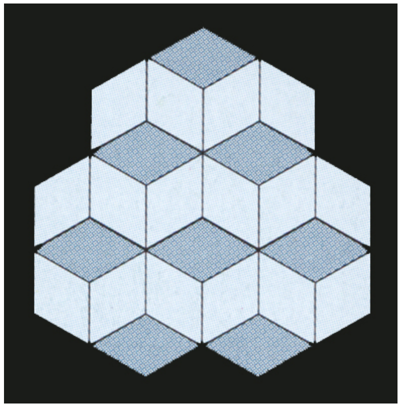

Figure 8. A bistable figure – an illusion of two interchanging perceptions which are evoked one after another by the same physical stimulus on the retina. A possible explanation is the consecutive activation of two different assemblies (attractors) within the visual brain.

change the perceived form. This reorganization might be provoked by a small movement of the eye or the attention searchlight (Wróbel 2000) independently directed by the voluntary brain processes.

The existence of neuronal assemblies whose activity represents complicated visual stimuli has been proven in many experiments. Such assemblies work as attractors, and can encompass a large number of cells located in different brain areas (Fig. 9). These attractors appear in the neuronal network of the brain during subjective

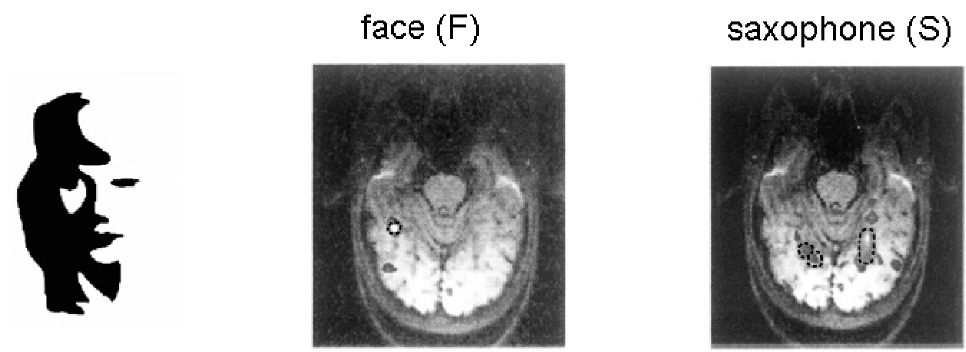

Figure 9. Cortical regions activated during alternating perceptions of face or saxophone (seen in fMRI). Based freely on data from Kanwischer et al. (1997).

experience by reinforcing internal connections within the forming assemblies that are activated frequently, and weakening the ties of the ones which are seldom used. As each of us has her or his own unique visual experience, there are no two brains alike among billions of people and also no two similar "true" worlds. A well-known picture, widely available on the internet, gives another example of the subjective (i. e. depending on experience) way of perceiving the world (Fig. 10). It is claimed that in this picture children under five years of age at a first glance see only nine dolphins in a bottle!

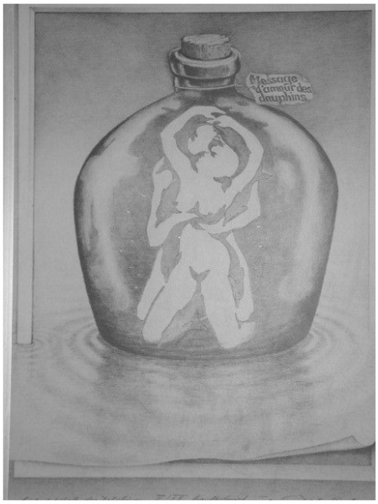

Figure 10. The perception depends on experience which forms the connections between neurons during development of the functioning brain. In this picture found on the Internet small children at a first glance see only nine dolphins in a bottle.

During the process of seeing, the activity of the visual brain is constantly being switched from one attractor to another in a continuous process of fast snapshots. They are seldom longer then a third of a second – the average inter-saccade time. It is still debated whether the brain builds up its subjective internal representation of the world on the basis of these snapshots (classic theories), or whether it rather utilizes the snapshots for immediate behavior with the possibility of reflecting on the external reality in its only true representation – that is, that reality itself (Freeman 1999, O'Regan and Noe 2001). Whichever is the ultimate integrative mechanism, the brain is constructed largely by actual personal experience (and thus for example does not allow easy comprehension of "impossible" forms (Fig. 11)).

Neuroinformatitians estimate that the amount of information transduced every second in the receptors of all sensory systems is about 10^9 bits, with only 100 bits actually consciously perceived. Most of this information is used for automatic control of our behavior or filtered out by mechanisms of lateral inhibition. This implies that we will never be able to acquire a real picture of the surrounding world, which we routinely call "the truth" seen by the "naked eye". At the same time, however, the plastic machinery of our brain allows us to survive and to enjoy the perception of the world carefully translated for our brain's subjective use.

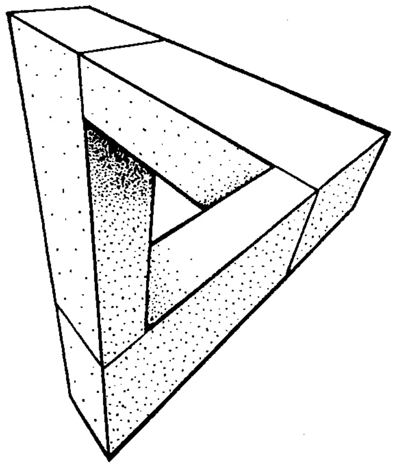

Figure 11. The "impossible" form is perceived without success. It provokes a repulsive emotion of something strange.

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