Article

Current Thoughts on the Neurology of Vision

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During 1994, four very significant books that impact our understanding of vision were published. Two of the books were written by Nobel Laureates currently working in fields that differ from the fields in which they won their prestigious prize. The third was written by a neurologist, whose writing style is a cross between Agatha Christie and Oliver Sacks, and the fourth book was circulated at the January 1994 Skeffington Symposium. This article presents a synthesis of ideas, concepts, and notions derived from all four books and from my previous papers on artificial intelligence,[1,2] chunking,[3] and *Wet Mind*.[4] These books have enriched my understanding of how our neurology supports the behavioral concepts of vision. The following is a synthesis of these books into a more comprehensive view of the neurological substrate of vision.

In late 1992, I read an article by Lawrence Weiskranz, of Oxford University, on a phenomenon called blind sight.[5] The article, "Unconscious Vision, The Strange Phenomenon of Blindsight," was published in *The Sciences* the September/October issue. In it Weiskranz stated, "To date, workers have identified nine branches of the optic nerve that connect with regions of the brain other than the visual cortex. One relatively large branch, which runs to a midbrain area called the superior colliculus, looks like a good candidate for mediating blindsight."[5(p27)]

Weiskranz pointed specifically to the branch of fibers leading to the superior colliculus as the underlying connection that most likely facilitated blind sight. Blind sight is the condition in which, after a stroke leaving a person with a single side hemianopsia (and without any conscious awareness of seeing in the hemianopic field), that person can, when asked, correctly guess colors and object names and even reach for specific objects in the hemianopic field. In blind sight, the raw data, which are processed further to yield "what is it" and "where is it" information, are somehow made available to the person to derive meaning and direct action, but not to inspect consciously. Because the visual cortex areas, due to lack of blood flow, have ceased to function, the information must be getting to the appropriate places in the brain via collateral connections. Weiskranz points to the 20% of the fibers leading to the superior colliculus.

At about this time, I read *Bright Air, Brilliant Fire, On the Matter of the Mind* by Gerald M. Edelman.[6] Edelman, Director of Neurobiology at the Scripps Research Institute, received the Nobel Prize for Physiology or Medicine in 1972. I had just finished *Complexity,*[7] a book in which M. Mitchell Waldrop discussed the concepts of self-organizing systems and the need for some underlying complexity in a system to allow the emergence of organized behavior of that system, and to endowing that same system with the ability to generate new behaviors to meet the changes of its environment. Edelman stated, "The brain is an example of a self-organizing system."[6(p25)] He also stated, "Diversity must inevitably result from the *dynamic* nature of topobiological events. The existence of diversity at the level of the individual animal is of great importance. Indeed, it is likely to be one of the most

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important features of the morphology that gives rise to mind."[6(p64)] "Individual variance in a population is the source of diversity on which natural selection acts to produce different kinds of organisms."[6(p73)]

Edelman asked, "How can an animal initially confront a small number of 'events' or 'objects' and after this exposure adaptively categorize or recognize an indefinite number of novel objects as being similar or identical to the small set that it first encountered?"[6(p28)] Edelman continued to identify what he calls the homonculus crisis, which he defined as the unitary appearance to a perceiver of perceptual processes that are known to be based on multiple and complex parallel subprocesses and on many neural maps.

The old diagrammatic representation of the brain from OEPF demonstrated the problem well. We now know that the information from the senses goes to many separate brain centers and is processed in parallel. Does the information ever actually get back together in one place and somehow become merged into an object concept? This is one of the most fundamental questions being asked in the study of the brain and mind today.

Most of the rest of Edelman's book was devoted to a treatise on Neural Darwinism which explains the evolution of the human brain and its morphology. Edelman stated that what is special about brains is evolutionary morphology. "Nervous system behavior is to some extent self-generated in loops; brain activity leads to movement, which leads to further sensation and perception and still further movement."[6(p29)] He stated further that, "There is no explicit information transfer between the environment and organisms that causes the population to change and increase its fitness."[6(p74)] This agrees well with the concepts that Harry Wachs and others have espoused for years, that there is no information in the light. We derive our understanding from what we have learned and developed within ourselves as a result of the experiences that we have had over time. Without the inner light of mind, the light from the environment will call forth no meaning. Continuing along the path of Neural Darwinism, Edelman stated, "Evolution, acting by selection on populations of individuals over long periods of time, gives rise to selective systems *within* individuals. Such selective systems acting in one lifetime in one body are called somatic selective systems. Thus, an evolutionary selective system selects for a somatic selective system!"[6(p74)] Thus, he has shown that what Darwin put forth for the evolution of the species has now been transformed to occur within a single person, allowing the evolution of the "species" of brain processes which leads to the emergence of consciousness and the mind.

Everything for Edelman comes together in his Theory of Neuronal Group Selection (TNGS). The three tenets of TNGS are shown in Figure 1.[6(p84)]

The first step is the development of the primary repertoire. A primary repertoire is, "a population of variant groups of neurons in a given brain region, comprising neural networks arising by processes of somatic selec-

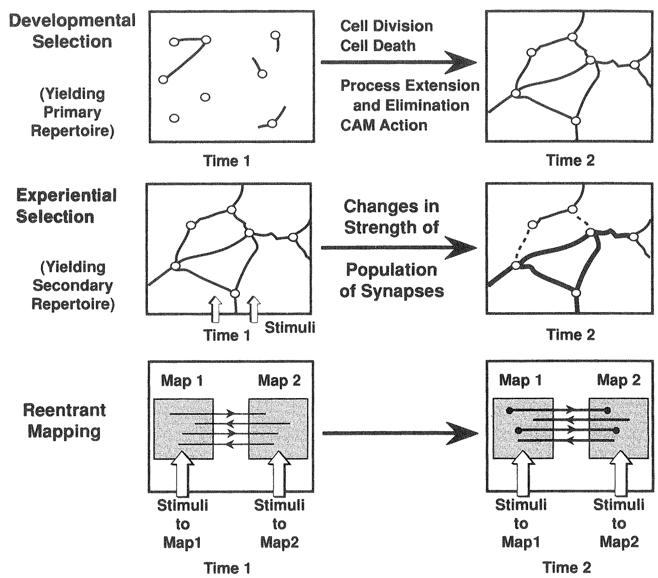

Fig 1. A selectional theory of brain function. Called the theory of neuronal group selection, it has three tenets. Top: Developmental selection. This occurs as a result of the molecular effects of CAM and SAM regulation, growth factor signaling, and selective cell death to yield varied anatomical networks in each individual, networks that make up the primary repertoire. Center: Experiential selection. Selective strengthening or weakening of populations of synapses as a result of behavior leads to the formation of various circuits, a secondary repertoire of neuronal groups. The consequences of synaptic strengthening are indicated by bold paths; of weakening, by dashed paths. Bottom: Reentry. The linking of maps occurs in time through parallel selection and the correlation of the maps' neuronal groups, which independently and disjunctively receive inputs. This process provides a basis for perceptual categorization. Dots at the ends of the active reciprocal connections indicate parallel and more or less simultaneous strengthening of the synapses in reentrant paths. . . . Strengthening (or weakening) can occur in both intrinsic and extrinsic reentrant connections (from Edelman[6]).

tion."[6(p83)] These areas are analogous to the small "f" functions I reported in the *Wet Mind* paper[4] presented in 1993. During this phase the theory of complexity rules predominates, and little outside influence is felt. Micro forces are at work establishing the substrate on which the further development of the brain and the emergence of consciousness and mind will depend.

Next we move into the phase of experiential selection, which I also covered extensively in the *Wet Mind* paper. . . . "During behavior, synaptic connections in the anatomy are selectively strengthened or weakened by specific biochemical processes. . . . Such a set of variant functional circuits is called a *secondary repertoire*."[6(p83,85)] It is here that the weights of the connections are modified. This represents the octopi neural network and the changes that have occurred over time as a result of the changing input-output-feedback conditions that occurred surrounding the network.[4]

The third phase is called reentrant mapping. The primary and secondary repertoires form maps. "These maps are connected by massively parallel and reciprocal connections."[6(p85)] "Reentrant signaling occurs along these connections. As groups of neurons are selected in a map, other groups in reentrantly connected but different maps may also be selected at the same time. Selective coordination of the complex patterns of interconnection between neuronal groups by reentry is the basis of behavior."

Figure 2 schematically demonstrates the interconnections between some of the visual areas. Of note is the fact that connections from V1, the visual cortex, are also shown to go back to the lateral geniculate. Pribram, in his book *Brain and Perception,*[8] noted that 8% of the optic nerve is efferent and that this 8% affects 80% of the afferent signals carried in the optic nerve. This shows completely the connections up and down the system from the retina to the brain and back again.

Edelman stated that perceptual categorization occurs "by coupling the outputs of multiple maps that are reentrantly connected to the sensorimotor behavior of the animal. Such a global mapping ensures the creation of a dynamic loop that continually matches an animal's gestures and posture to the independent sampling of several kinds of sensory signals."[6(p89)] "Sensorimotor activity over the whole mapping selects neuronal groups that give the appropriate output or behavior, resulting in categorization."[6(p90)] Figure 3 shows

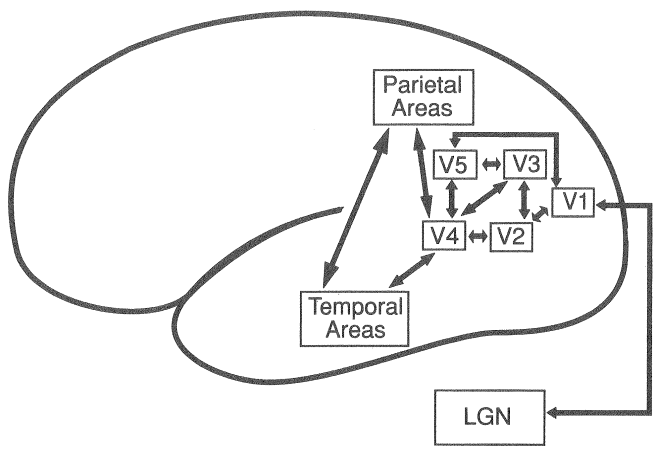

Fig 2. Multiple maps of visual areas of the brain are reentrantly connected to each other (see double arrows linking visual maps V1–V5, the temporal areas, and the parietal areas). Each map serves in a functionally segregated manner—for color, motion, orientation, and so forth. No "supervisor map" exists that summarizes "information" on these properties. But as a result of reentry (the double arrows), the maps act coherently to respond to combinations of properties. Even the region known as the lateral geniculate nucleus (LGN), an infracortical region that receives signals from the optic nerve of the eye, is reentrantly connected to the primary visual map, V1 (from Edelman[6]).

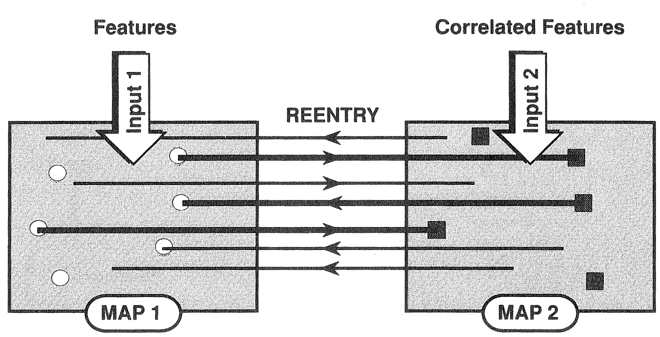

Fig 3. Reentry. Two maps of neuronal groups receive independent inputs (1 and 2). Each map is functionally segregated; that is, map 1 responds to local features (for example, visually detected angles) that are different from those to which map 2 responds (for example, an object's overall movement). The two maps are connected by nerve fibers that carry reentrant signals between them. These fibers are numerous and dense and serve to "map the maps" to each other. If within some time period the groups indicated by the circles in map 1 are reentrantly connected to the groups indicated by the squares in map 2, these connections may be strengthened. As a result of reentrant signaling, and by means of synaptic change, patterns of responses in map 1 are associated with patterns of responses in map 2 in a "classification couple." Because of synaptic change, responses to present inputs are also linked to previous patterns of responses (from Edelman[6]).

this type of mapping represented schematically. In a later reference, on can see specific layers in the LGN being mapped to specific layers in V1, in addition to specific layers from V1 going back to different layers in the LGN.

Figure 4 shows the level of interconnectivity, the end result of which is movement, movement that is necessary to alter the organism's sampling of the environment.

What evidence did Edelman give for reentrant loops? First, he presented the discovery of all the parallel connections. This is well and good, but just because something is wired one way does not mean that that way is how the wires are really used. He reported on the work of Wolf Singer, Reinhard Eckhorn, and their colleagues, whose works have shown coordinated firings in different areas of V1 and V2 occurring at exactly the same frequency, 40 cps, with their phases being the same.

Edelman then discussed the role of the limbic system, which is involved with homeostatic, appetitive, and consummatory needs reflecting evolutionarily established values. These included the hypothalamus and various

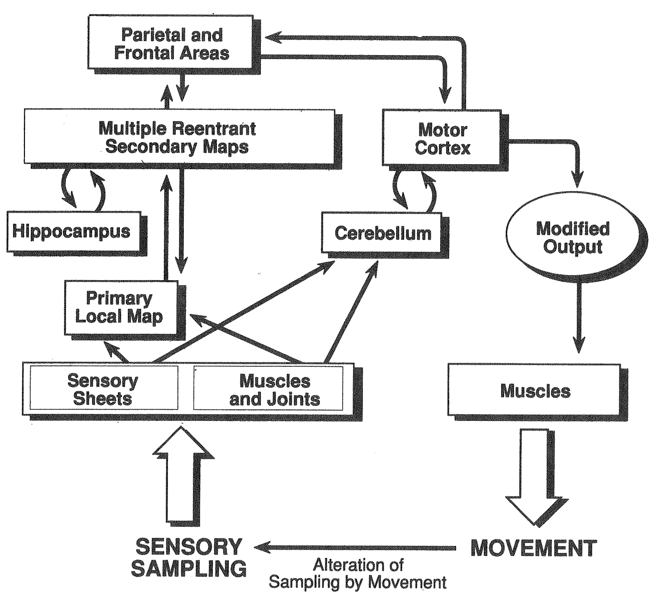

Fig 4. A global mapping. This structure is made up of multiple maps (of the kind shown in the previous figure). The maps are also connected to brain regions such as the hippocampus and cerebellum. Notice that signals from the outside world enter into this mapping, and that multiple sources of output lead to movement. This in turn alters how sensory signals are picked up. A global mapping is thus a dynamic structure, one that changes with time and behavior. Its reentrant local maps, which correlate features and movement, make perceptual categorization possible. Perturbations at different levels cause a global mapping to rearrange, to collapse, or to be replaced by another global mapping (from Edelman[6]).

nuclei in the midbrain, including the lateral and medial geniculate and the superior colliculus. They involved regulation and the control of certain set points about which balances were established. "Learning is achieved when behavior leads to synaptic changes in global mappings that satisfy the set points."[6(p101)]

These circuits can be divided into two types. The first are the limbic to brain stem functions that regulate heart and respiratory rate, sweating, digestive functions, as well as bodily cycles related to sleep and sex. These circuits are often arranged in loops that respond slowly (in periods ranging from seconds to months) and that are not highly detailed in their mapping. The connections have been shaped to match the needs of the overall body and not to meet large numbers of unanticipated signals from the outside world.

The second set of connections of the limbic system are the thalamocortical systems. These connections respond extremely quickly. Instead of involving a few reentrant circuits, the connections are much more highly connected, layered local structures, with massive reentrant connections. It is from these connections that Edelman believes primary consciousness emerges. He stated, "We experience primary consciousness as a 'picture' or a 'mental image' of ongoing categorized events. But, there is no actual image or sketch in the brain."[6(p119)]

Moving on, we get into a discussion of *qualia,* the personal and subjective experiences, feelings, and sensations that are part of awareness. The study of qualia, such as color, emotions, temperature, and many others are central to understanding the many rifts between psychology and neurology. Qualia are experienced directly only by individuals. "*We cannot construct a phenomenal psychology that can be shared in the same way as a physics can be shared.*"[6(p114)] Because nearly all vision consists of such qualia, we are left with the nearly impossible task of attempting to build a "science" of vision to explain what we do, which is testable in a manner similar to physics. I believe that Edelman and others clearly are making the case that we will never be able to do this at the level of qualia. However, his approach is an extraordinary one because it provides us with the direct neurological support of the behavioral concepts of vision.

The Edelman book was a bit difficult at

times and Greg Kitchener (personal communication) suggested I look at a book entitled *The Man Who Tasted Shapes*[9] by Richard Cytowic. I interrupted my reading of Edelman and became enveloped by Cytowic's style, which is much like that of a mystery writer. He wrote of the disease called synesthesia which means "feeling together." Synesthesia is the strange situation where stimuli in one sensory modality will elicit responses in a completely different sensory area. Here the qualia are all mixed up. However, the associations for a particular person are usually mapped in a fairly consistent way, so that from one experience to another the joined qualia are the same. Cytowic recounted the years of experience and investigation that he had with his friend, and then patient, Michael. Cytowic believed strongly that by understanding synesthesia we might actually learn how we come to build a consistent view of our world. He felt that the implications of understanding synesthesia go far beyond the entity itself, and provide insight into how we all experience and interact with the environment.

One very interesting idea, which I found echoed by Arthur Zajonc in *Catching the Light,*[10] is the notion of qualia as it relates to color constancy. He stated that, "The constant appearance of objects under widely varying conditions of illumination, intensity, and wavelength distribution is a well-known psychological issue and a central theme in understanding how we see. Because the predominant color of daylight changes from blue to red from sunrise to sunset, the same things viewed in the morning should look bluer than they do in the evening, when they should appear redder. People never notice this dramatic physical change. Instead, we perceive the color of an object as constant. Even when the change is huge, as it is when we step from outside to indoors, colors still look constant."[10(p61)]

The flip side of color constancy is the fact that colored shadows work in entirely a different manner. In color constancy, different stimuli look the same. When looking at shadows, the same things will look different. Zajonc stated that, "All shadows have color, which is complementary to the illuminated side." He then continues and asks the provocative question relating to qualia in general: "Why do the rest of us appear to agree so well when there is not compelling basis for agreement?"[10]

An interesting part of qualia is that there are quite a number of qualia that are common to several senses. For example, we can both see and feel the size of an object and we can both see and hear the movement of an object from one place to another. These qualia are not triggered by a single sense but can be triggered by multiple senses. How than are they associated? Are they sent along to a common area? The answer here is a resounding, "No!" There is obviously some manner in which events in different parts of the brain are coordinated and can be triggered from either side or from many different directions. Here is where we see the need for all the double-headed arrows on the diagrams and the interconnectivity of the many different sections of the brain.

Cytowic made some statements that I found particularly interesting. "We have known for a long time that the ability to make cross-modal associations is the foundation of language; because of this we can assign names to objects. Cross-modal associations are a normal part of our thinking, although they occur at an unconscious levels."[9(p96)] We develop this at a very young age. If we show a 2-year-old an object and then put him in the dark, he can identify the object simply by feeling it and he recognizes it as the same as the object he had only seen before. These cross-modal associations are essential in the formation of object concepts.

A series of experiments helped Cytowic locate the possible-site at which the synesthesias were occurring. He found that, in situations in which cortical functions were stimulated with an amphetamine, the occurrences of synesthesia were reduced significantly. However, if cortical function was depressed with alcohol or with amyl nitrate, the synesthesias increased dramatically. This helped to steer Cytowic away from the cortex as the site of the synesthesias.

Blood flow studies during synesthesia showed some incredible results. During synesthesia, the average blood flow in the left hemisphere of his patient Michael dropped to three times below the lowest acceptable limit of an average person! Although the left side of the brain's blood flow nearly shut off, there was a net increase in flow for the entire brain. Where was the brain metabolism increasing? In the limbic system. Cytowic viewed the limbic system as the final arbiter of the brain. Here is where the synesthesia was occurring and where much coordination of that which we attend to is taking place.

Cytowic's new view of how the brain works is summarized here:

1. The flow of neural impulses is not linear, but parallel and multiplex, including transfer of information that does not even travel along nerves.
2. We no longer speak of localization as a one-to-one mapping, but of the distributed system; a many-to-one mapping in which a given chunk of brain tissue subserves many functions and also, conversely, by which a given function is not strictly localized but is distributed over mare than one spot.
3. While the cortex contains our model of reality and analyzes what exists outside ourselves, it is the limbic brain that determines the salience of that information.
4. Because of this, it is an emotional evaluation, not a reasoned one, that ultimately informs our behavior."[9(p156)]

Thus, it is the limbic system that acts as a valve. It decides what will grab our attention at any particular time. The pervasiveness of the connections from the limbic system is shown in that humans have five times as many fibers in a single limbic pathway called the fornix than in both optic nerves combined. Cytowic stated that, "I believe that synesthesia is actually a normal brain function in every one of us, but that its working reaches conscious awareness in only a handful."[9(p166)] "The limbic brain remains the terminal stage of information processing, that stage for suppressing automatic, habitual responses in favor of new alternatives when the unexpected happens."[9(p168)]

Cytowic was likening the role of the limbic system to that of a critic. It sits back and evaluates what is going on to determine what is relevant or not. To do this it must be processing at a much higher rate of speed than the rest of the brain. Is there any evidence of this? He stated that, "The limbic system performs calculations at an internal cycles-per-second rate of 400 Hz." The limbic system is governed by an outer clock rate of 5 Hz, which happens to be the theta rhythm. The cortex is governed by an outer clock rate of 10 Hz, which is the alpha rhythm. "This 2:1 ratio is what engineers require to adapt a critic. You need to hold, store, and reevaluate in a way that makes the cycle time of the critic twice as long as the model's cycle. This 2:1 ratio exists between the limbic brain's evaluation and the update of the model in the cortex in the following way: the state of the world is pumped into the cortex and an evaluation comes out one fifth of a second later, yet elements inside the limbic system are cycling furiously 400 times a second to carry out the intermediate steps needed to derive that evaluation."

The most recent of the books was brought to my attention by a group of international guests who had camped out in Borders bookstore one evening. They highly recommended a book entitled *The Astonishing Hypothesis, The Scientific Search for the Soul* by Francis Crick,[11] the Nobel prize winner who discovered the structure of DNA with James Watson. My guests were saying that this book was all about vision; they were right!

Much of Crick's book agreed with Edelman and Cytowic, so I will highlight just those areas where he has gone one step further. It should be noted that Crick had the advantage of time because his book was published after the other two. It is obvious that he is fully aware of Edelman's work, but not of Cytowic's. They still came to much the same conclusion.

Early in the book he used the word "emergent" to describe the behavior of the brain. He stated that, "emergent behavior cannot in any way, even in principle, be understood as the combined behavior of its separate parts. The scientific meaning of emergent, assumes that, while the whole may not be the simple sum of the separate parts, its behavior can, at least in principle, be understood from the nature and behavior of its parts plus the knowledge of how all these parts interact."[11] Vision itself is an emergent which we understand by understanding the subprocesses and how they interact with each other.

A few statements from Crick set the stage early on. He stated, "We really have no clear idea how we see anything. We do not yet know, even in outline, how our brains produce the vivid awareness that we take so much for granted. It is easy to show that how you think you see things is largely simplistic or, in many cases, plain wrong. The photons coming into our eyes only show us how much light comes from each particular part of the visual fields, plus some information about its wavelength."[11(pp24–25)] "It is difficult for many people to accept that what they see is a symbolic interpretation of the world-it all seems so like 'the real thing.' But in fact we have no direct knowledge of objects in the world."[11(p33)]

In 1992 I presented a paper on the space world in which I spoke about an attention ball as a way to illustrate, out in space, the area of space which a person selects to attend to.[12] I stated that the attention ball could be contracted into a small place in space when one wanted to inspect a small area for detail, or that the attention ball could be expanded outward to take in information from a rather large amount of space. Crick used the analogy of a search light or a spotlight for attention. "Inside the spotlight the information is processed in some special way. This makes us see the attended object or event more accurately and more quickly and also makes it easier to remember."[11(p62)]

From the data that we take in we build an internal representation of reality. When talking about short-term memory Crick quoted the Israeli neurobiologist Yadin Dudai, who stated that the "internal representation of the world—that is, of both the external and internal milieu is neuronally encoded and structured which could potentially guide behavior. 'Learning' is then the creation or modification of such an internal representation, produced by experience."[11(p66)]

The exciting part of reading this book was that the more I got into it, the more Crick seemed to be talking directly to behavioral optometrists. For the most part, his view was consistent with the views that had come before, but he went further in elucidating the specific connections of vision than anyone who preceded him. First, he validated Cytowic's view of the importance of the limbic system. He also validated Edelman's reentrant loops. He talked about the different sections of the brain: "The most important of these is the thalamus, sometimes called the gateway to the cortex, because the main inputs to the cortex have to pass through it. The thalamus is conveniently divided into about two dozen regions, each of which is concerned with some particular subdivision of the neocortex. Each thalamic area also receives massive connections from the cortical areas to which it sends information."[11(p84)] "For example, a small group of neurons, called the 'locus ceruleus,' send signals to various places, including the cortex. A single one of these nerve fibers can extend from the front of the cortex to the back, making millions of connections to other nerve cells on the way."[11(p89)]

When Crick discussed the electrophysiology of vision from the standpoint of using the visual evoked potential, he confirmed some of the exciting adventitious adaptations made by the deaf to which Sacks refers in his book, *Seeing Voices, A Journey Into the World of the Deaf.*[13] Crick cited the work of Helen Neville which showed that in the deaf exposed to American Sign Language (ASL) at an early age "parts of the visual system take over parts of the hearing system during the brain's development."

Crick discussed in detail what occurs in the thalamic region and, in particular, what is the role of the superior colliculus. He believed that the main role of the superior colliculus is the control of eye movements, as well as controlling other aspects of visual attention. The colliculus is divided into three regions. "The upper regions receive various kinds of retinal input as well as input from the auditory and somatosensory systems." In the deep regions there are fibers which cross the midline that connect to the brain stem "onto neurons that lead to the control of the muscles of the eyes or the neck." As we can see here, some of the pathways postulated by Harmon[14] and discussed by Kraskin[15] are now being revealed.

How do the eyes know where to jump? Crick reported on the work of Sparks and Robinson. They showed that the middle and the deep regions of the colliculus had a 'motor' map rather than a sensory map. "The firing of neurons in these regions encode the direction and amplitude of the change in eye position needed for the eyes to make a saccade to the target."[11(p127)] "To produce a saccade, a patch of collicular neurons starts to fire rapidly. Broadly speaking, it is the center of this activity in the motor map that determines the jump vector. Thus, a particular single collicular neuron may take part in many rather different kinds of jumps. It is the active neurons as a whole that determine the vector nature of the saccade. In short, the control of a single eye movement is controlled by many neurons."[11(p128)] The advantage of this type of system, like other neural networks, is that damage to any one cell or even small groups of cells will not affect the functioning of the system.

Consider the LGN. The LGN is surrounded by a thin sheet of cells called the reticular nucleus of the thalamus, which is different that the reticular formation. The influence of the reticular nucleus is inhibitory; the reticular nucleus is thought to be the guardian of the gateway. Steve Cool[16] has called this the gating system, which may play a very significant role in both suppression and amblyopia, as well as other binocular disturbances. Crick confirmed the work of Edelman and Pribram in his discussion of the fibers that lead from V1 back to the LGN. He stated, "Surprisingly, there are many more axons coming back from V1 than going up to it, but they tend to synapse onto those parts of the dendrites rather distant from the cell bodies of the LGN neurons, so their effects may be rather subdued."[11(p131)] He also stated that there are inputs that also come from the brain stem area which modulate the behavior of the thalamus and, in particular, the reticular nucleus of the thalamus.

Figure 5, which is from Crick's book, shows V1 and just a few of the connections that come in and out of it. The inputs from the LGN go primarily to layer 4, with some coming into layer 6. The synapses in layer 4 are all excitatory. A discussion of the parvo and magno cellular division was included in the text, but is too lengthy to include here. The interconnections between V1 and V2 were also interesting. There are almost as many neurons that go from V2 back to V1 as come from V1 to V2, but there is an important difference. The fibers coming from V1 to V2 terminate mostly in layer 4 in V2. However, the fibers going from V2 back to V1 totally avoid layer 4 in V1.

Figures 6 and 7 have been included for the reader's interest. Figure 6 shows a proportional sketch of the brain divided in such a way that it could be laid out flat. The sections that are shaded deal with vision. Figure 7 is a schematic of the connections throughout just the visual parts of the brain.

Crick entered the blind sight foray with some very astute observations. First, he stated

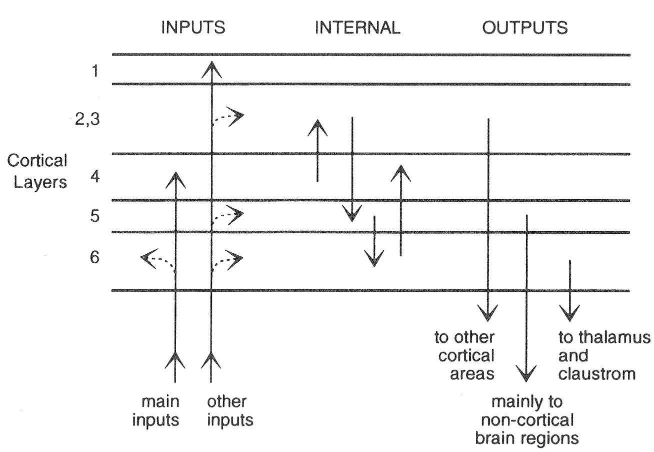

Fig 5. A grossly simplified diagram showing some of the major pathways within cortical area V1. There are many sideways connections that are not shown in this diagram (from Crick[11]).

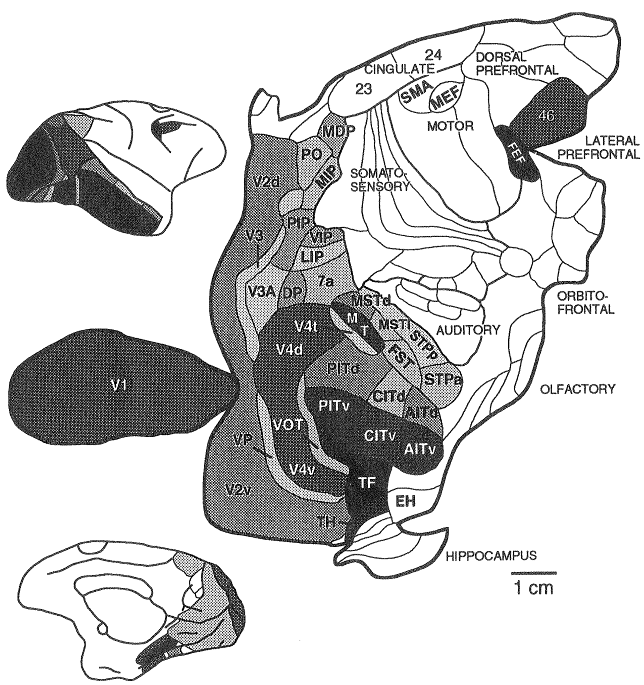

Fig 6. The main drawing shows the many different cortical areas on one side (here the right-hand side) of the macaque's brain. The two smaller figures (on a smaller scale) on the left show the view from the outside (the upper one) and from the inside (lower one), as if the brain was cleaved in half. The cortical sheet has been unfolded. . . . The many areas connected with vision are shaded. Their various names, abbreviated in most cases to initials, are shown in the figure. Their interconnections are shown in [*Fig 7*]. The main flows of information are broadly from V1 (on the left) toward the areas on the right of the figure, especially those on the bottom right (from Crick[11]).

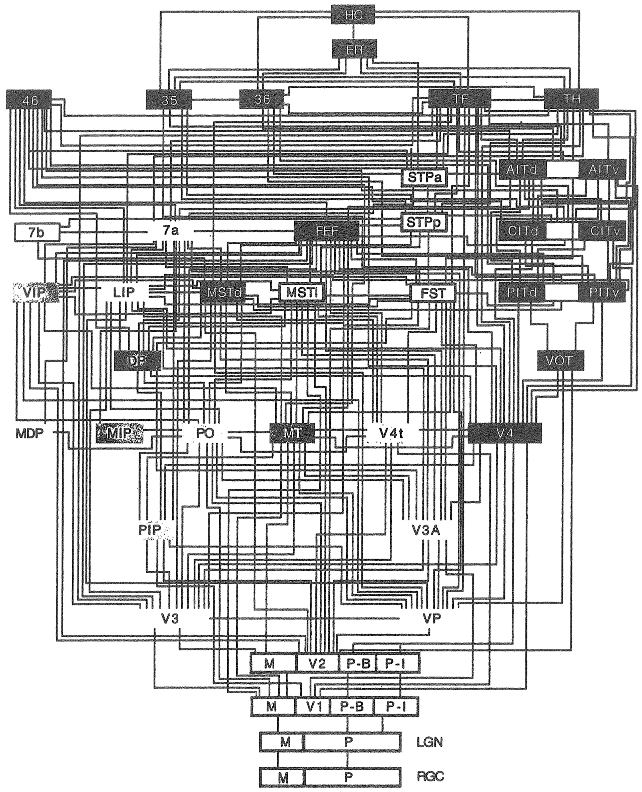

Fig 7. This figure shows the many connections between the different visual areas. It uses the convention . . . that each line represents many axons, running in both directions. At the bottom of the figure, labelled RGC, are the retinal ganglion cells in the eye. LGN is part of the thalamus. This projects to the first visual area, V1, shown subdivided into four parts, with the second visual area, V2 (also in four parts), just above it. The names of the different areas are fairly arbitrary and need not concern the reader. At the top, HC stands for hippocampus and ER for the entorhinal cortex that leads into it. The arrangement is semihierarchical, as explained in the text. Many other (nonvisual) cortical areas, shown in [*Fig 6*], are not shown in this figure. Modified by Suzuki and Amaral from Felleman and Van Essen (from Crick[11]).

that the superior colliculus only obtains cells from the magno cellular system, which does not carry information about color for the cones. Yet, victims of blind sight seem to be able to discern color in the affected field. Thus, the views of Weiskranz and Edelman must be incomplete. Crick stated, "There are direct though weak pathways from the LGN directly to areas in the cortex beyond V1, such as V4. These pathways may remain sufficiently intact to lead to a motor output (being able to point, for instance), but not enough for visual awareness."[11(p173)] For this reason, it may take days to months after the stroke for the phenomenon of blind sight to appear. The more these alternate pathways are used over time, the stronger they become, until they are useful. This explains a great deal about how a person who has had a stroke adapts over several months to the point where, even though an absolute field loss can still be demonstrated in field testing, many can navigate through their environment as if the full field were responding normally. They can be taught to learn to trust what they are not aware of seeing, and can begin to function much more normally than if they are told that they will never regain any use of their vision on the affected side!

Crick's discussion of plotting receptor fields of the visual cortex was very interesting. Karl Pribram, at a meeting for optometrists several years ago, showed some disdain for the work of Hubel and Wiesel. He stated that their work was far too simplistic and that their core concept of cells and their receptor fields was incorrect. He stated that each cell was part of multiple overlapping receptor fields, that in one instance might react to orientation but in another to contrast, and in yet another to orientation. Crick stated, "One cannot deduce the function of a neuron in the brain merely by looking at its receptive field."[11]

Crick also discussed consciousness and what has already been called the binding problem. We know that things do not come back together in a single area in the brain for viewing or for understanding. He stated, "The brain in some way binds together, in a mutually coherent way, all those neurons actively responding to different aspects of a perceived object."[11(p208)] Crick agreed with the others cited here who believed that we can only pay attention to one object at a time, although this is not what we experience phenomenologically.

His theory related to what he called correlated firing. Figure 8 shows the firing patterns for a red circle and blue square in the primary visual field at the same time. Here the interest is in the 40-Hz oscillations in the limbic system. The 40 Hz here is not clearly related to the 400 Hz internal oscillations seen by Cytowic. Crick saw this as a possible answer as the coordinator of the binding problem. Crick cited the work of two groups in Germany, led by Singer and Gray, who proposed that the neurons symbolizing all the different attributes of a single object would bind these attributes to each other by firing together in synchrony. Crick, and his assistant Koch, went

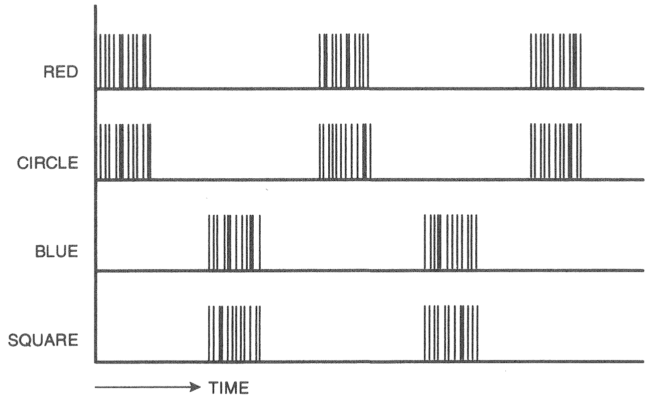

Fig 8. Each short vertical line represents a neuron firing at some moment in time. The first horizontal line shows the firing of a neuron that signals "red." The next line, one that signals "a circle," and so on. The brain can deduce that the circle is red, not blue, because the red neuron fires at about the same times as the circle neuron, whereas the blue neuron fires at very different times. This is expressed by saying that the firing of the "red" and the "circle" neurons are *correlated* (as is that of the "blue" and the "square" neurons), whereas the *cross-correlation* for example, between "red" and "square," is zero. (The example has been grossly oversimplified for didactic purposes.) (from Crick[11])

one step further and postulated that this synchronized firing might be the neural correlate of visual awareness. They further suggested that, "the main function of the attentional mechanism would be to select an object for attention and then help to synchronize the coalition of all the relevant neurons that corresponded to the brain's best interpretation of that part of the visual input. The thalamus, we surmised, was the 'organ of attention,' some parts of it controlling a spotlight of attention that hopped from one salient object to another in the visual field."[11(p245)]

The explosion of writings in the field of neurology and related sciences is leading us to a better understanding of how our visual abilities emerge and how the process of vision has evolved. As more is understood, the more solid the behavioral concepts of vision will become.

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