Biomedical Correlates of Human Vision

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Our perceptive apparatus conveys the impression that we see the world around us as a cogent whole, in reality we see a series of 'snapshots' from which we make a construct in our central nervous system. How do subjects pick the next object to examine? Through our peripheral retina, we are able to perceive the objects in the visual field and make a selection of the ones that may interest us. This shift of attention from one item to the next accompanies each saccade. It is not random: we can understand this when we look at painting where when we focus on the trees at the top of that painting, the grass at the bottom gets ignored. In sharp contrast, faces, dresses, and other significant objects are frequently inspected.

Alfred Yarbus,[1] a Russian genius and a neuropsychologist was the first to note the connection between eye movements and objects of potential interest to the observer. He suggested that the "location of saccades could accurately indicate attentional shifts. He concluded that the location of saccades was a good indicator of the subject's attentional shifts. Whether a particular object attracts attention or not is determined by a combination of that attributes associated with the object (its colour, motion, shape, brightness) and the subject's goals at a given moment. Attention is a very important factor in active vision — some might say the most crucial factor — because it determines where we look. The neuronal activities in the brain related to shifts in attention and the generation of saccades are closely linked".[1]

As Yarbus[1] states: "Active vision comprises several functions, but of course, it is only a small part of the larger brain systems involved with sensation and motor control. In turn, the puzzle of how these systems operate to produce action is just one of many global questions about how the brain produces all behaviour, including learning, memory, and emotion; and even how consciousness arises from brain activity. Considering active vision alone, however, exemplifies the classic approach of reducing the overwhelming complexities of the brain to more easily understood fragments. Galileo had to study the solar system before we could study the universe".[1]

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Neuronal Understanding of Human Vision

The preliminary step is to move from describing the benefits of saccades to accurately specifying the problems that these saccades can produce for human vision. Subsequently we can consider corollary discharge, a brain mechanism which eliminates the problems created by the saccades. Then we can review our basic knowledge of the brain pathways that process visual stimuli and produce saccadic eye movements in order to locate the source of a corollary discharge. Lastly, we consider how the corollary discharge circuits we find act to minimize the disruptions saccades can generate.

A saccade can produce two major problems for vision: blurring and displacement of the images.[2] Blurring occurs when the image of the scene is swept rapidly across the retina during each saccade while image displacement is closely related to blurring: The saccade moves the fovea centralis from one part of the visual scene to another leading to the image on the retina being displaced (analogy: a movie camera moving in rapid jerks from one spot to another). Curiously though these problems can be extremely troublesome, they are rarely encountered in clinical practise. A sizeable number of patients are aware of the blur that occurs during saccades, but hardly anyone is aware of the displacement of images on the retina. If these displacements were more visible, almost everyone would be seasick most of the time. These problems are because they arise at the fundamental source of all visual knowledge viz. the retina. And the manner in which this problem is resolved is one of the most sophisticated feats of information procession by the human nervous system.

Practitioners of natural sciences have speculated for centuries about why we experience visual stability rather than seasickness with rapid eye movements. Most neurophilosophers believe that there must be a mechanism in the brain that warns the sensory systems that a movement is about to occur. With this facility, the sensory systems would be appositely advised of the impending disruption and could compensate for its logical consequences. Hermann von Helmholtz, one of the premier visual scientists of the nineteenth century, called this an "effort of will," while others who subsequently studied the problem in the twentieth century referred to it as an "efference copy" or "corollary discharge".

The fundamental principle is that the same sensorimotor processing area that steers the movement—in this case the saccadic—which also produces a copy or corollary of this drive.[3] These signals are identical, but one leads to the movement command, while the other is directed toward other brain areas to advise them that the eye is getting ready to move. Recipient brain areas include those devoted to processing visual information, since they would receive the visual consequences of the saccade. As far as the saccadic eye movements go, the movement command that produces the saccade and the corollary discharge circuits almost certainly originate in the superior colliculus (a subcortical area deep within the brain). The corollary discharge is then directed to the cerebral cortex, which covers the surface of the brain and is the site of the highest levels of information processing underlying much of our behaviour. The concept of a corollary discharge is centuries old, but it is only in the last decade that we have begun to identify its neuronal implementation in brains similar to our own primarily through animal studies.

When we consider the neuronal circuits that underlie the corollary discharge in the human brain, the general belief is that such circuits can be identified using brain imaging, particularly functional magnetic resonance imaging (FMRI). However, because FMRI signals are derived from changes in blood flow that are averaged over several seconds, FMRIs are not adequate for investigating active vision. Over that period, the eye will have moved several times, changing the image on the retina with each movement and precluding FMRI records from capturing the rapid developments of active vision. The query though remains that if imaging does not help, how do we begin to understand the brain activity underlying our active vision?[4]

The solution is to study the organization of neurons in animals whose vision and eye movements are similar to ours. For active vision, the animal of choice for experimental purposes is the Old World monkey (the Rhesus monkey). These monkeys' visual discriminations and their range of eye movements are in most cases virtually identical to those of human beings. The relevant anatomical connections in human and monkey brains are also remarkably analogous. Painless recording techniques from brain neurons in monkeys while they perform a series of visual tasks have revealed changes in the brain during active vision. As of now, it is fair to say that most of what we know of the structure and function of the human brain for active vision is derived from studying the brains of Old World monkeys. Experiments in dozens of laboratories around the world have built up an outline of the brain systems that underlie the analysis of visual input, the transition between visual and motor systems, and the motor output–all key phases of brain activity supporting active vision.[5]

It has been successfully established that the neurons in the pathway in the monkey brain have activity identical to that in the human brain. The salient question is where do the pathways underlying active vision might a corollary discharge arise? The superior colliculus is such a site: it has the origin of commands to move the eye and a source of projections back to the cortex. Each of the senses and each internal signal have dedicated nuclei in the thalamus; thus, it is a basic feature of primate brain organization. To use an air travel analogy, every passenger flying to the cortex must change planes at the thalamus.[5]

Now that we have identified two corollary discharge pathways to the cortex, we can now investigate how they contribute to solving the two problems that saccades create for vision i.e. blurring and image displacement. The first problem is the blur resulting from each saccade. The simple answer is to: suppress visual activity during the saccade and blur is automatically suppressed as well. A century ago, we used to think that such suppression was produced by a "central anaesthesia" in which activity during the saccade was simply blanked out. When it became possible in the 1960s to record directly from monkeys' brains, it immediately became clear that neurons in the brain continue to respond to visual input quite well during saccades. We have determined some suppression of neuronal activity during saccades.[6]

Blur vision can also result from a phenomenon called visual masking: when a dim object is preceded or followed by a bright object, the dim object is not seen. Similar masking effects are often seen working on neurons within the primary visual area. This occurs only in a well-lit environment, though it is highly effective. Masking of dim objects can occur any time bright objects are also present even when we do not observe any eye movements.[6]

Corollary discharge also contributes to the suppression of neuronal activity in neurons. For instance, the neuron responds to a stimulus moving in front of the stationary eyes (left) but not when the moving eyes pass over a stationary stimulus (right). The response is merely suppressed during the attention movement and therefore the corollary discharge is merely present when the attention moves. The suppression, therefore, is correlated with the saccadic eye movement. This suppression must be driven by a corollary discharge rather than visual masking, because masking only functions in the light and the corollary discharge-related suppression was demonstrated in the dark.[6]

The second problem for vision which will be ameliorated by the action of a corollary discharge is that the

displacement of images on the retina with each saccade. But here the neuronal mechanisms are substantially more complicated than those used for blur suppression. To understand these mechanisms which will affect image displacement, we must briefly consider how visual information is organized within the brain. Visual processing starts when the image of a visible scene falls on the retina and forms a retinotopic map; that's a layout of the visual scene is mapped on the retina just as it exists in reality.[7]

An explanation of perceived visual stability is that the retinotopic map is simply updated after each saccade. This hypothesis relies on experimental observations of single neurons in the parietal and later the frontal cortex. As the monkey fixated on an object, a lightweight was flashed within the receptive field. This produced a visual response. Very unexpectedly, this also activated the neuron.

Current Status of Biomedical Research

Goldberg and Wurtz[8] point out: "Active vision is one of the first examples of a system in our brain that is neither sensory nor motor as we previously imagined ; rather, its whole function depends on the synchrony between visual input, movement output, and systems internal to the brain, such as those for corollary discharge. This organization allows primates to use the high-resolution fovea to look at anything anywhere within the field of vision. The price paid is that eye movements generate major problems for the sensory system two to 3 times per second. While these problems originate at the very first stages of the sensory system, the solutions do not: they're spread throughout the sensory system across wide regions of the brain, including the very best levels of visual processing within the parietal and frontal area".[8]

Moore *et al* [9] in their widely quoted paper state: "Active vision creates two significant problems – blurring and displacement of retinal images – and there are two identified brain circuits that might contribute to the solutions. Both circuits rely on a corollary discharge derived from the brain areas where commands to move the eyes originate. One circuit extends from the center to the visual area and should provide an input to the cortex that suppresses blur during saccades. The second circuit connects the center and therefore the frontal area and should provide the anticipatory activity that warns the frontal area that an interruption of visual input is about to occur as a result of the subject's own eye movements". [9]

Golberg and Wurtz[8] summarise the current state of neuro-ophthlamology as : " the process used to explore the neuronal basis of active vision is an excellent illustration of how neuroscientists go about identifying the neuronal mechanisms that underlie behaviour. As we've seen, the study begins with the quantification of behaviour that's straightforward for active vision, because methods for measuring eye movements and psychophysical measurements of visual perception are both readily available. The second step is to determine a correlation between the measured behaviour and neuronal activity within the brain. Analysis of active vision, for instance, depends on the extensive correlations established between behaviour and neuronal activity undertaken over the last century, first on the sensory system then , when recording eye movements became possible, on the visual-motor system".[8]

Moore *et al* [9] have very astutely inferred: "The final step, and frequently the most elusive one, is to develop a precise model that represents the elements of the System and that predicts its functions: both those known and people so far unrecognized. We currently have only a glimpse of the neuronal basis of active vision within the brain. However, even with the limited methods we've now, an understanding of the system's organization seems reachable. The hope is that active vision becomes an example of how a complex problem is solved by the brain in simple and clever – but not necessarily intuitive ways".[9]

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