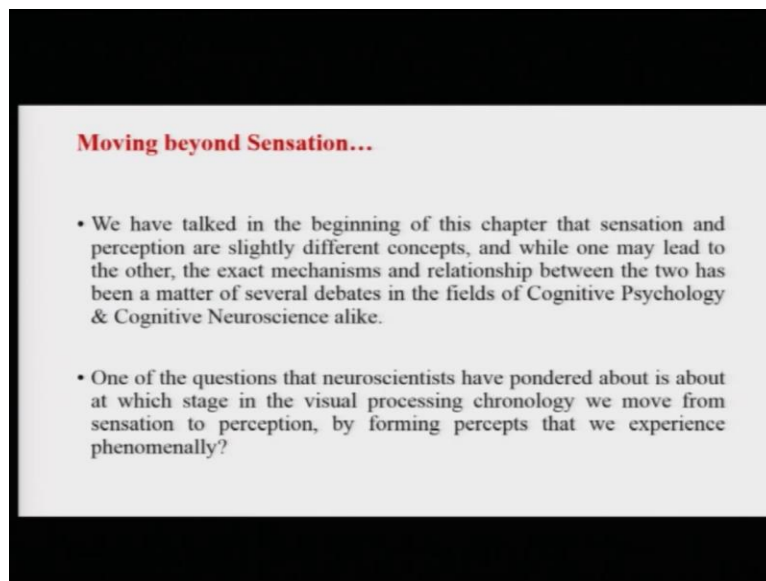


Introduction to Brain & Behavior
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Lecture 15 - Neuroscience of Sensation and Perception

Hello and welcome to the course, Introduction to Brain and Behavior. I am Dr. Ark Verma from IIT, Kanpur. As you know, I work at the Department of Humanities and Social Sciences and also at the Interdisciplinary Program of Cognitive Sciences at the institute. This is the final lecture of the third week. And we are talking about neuroscience of sensation and perception.

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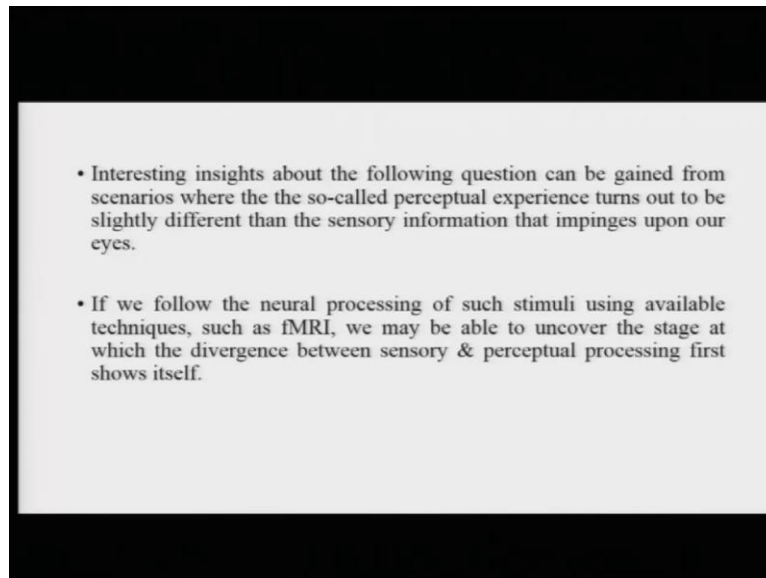


Moving beyond Sensation...

- We have talked in the beginning of this chapter that sensation and perception are slightly different concepts, and while one may lead to the other, the exact mechanisms and relationship between the two has been a matter of several debates in the fields of Cognitive Psychology & Cognitive Neuroscience alike.
- One of the questions that neuroscientists have pondered about is about at which stage in the visual processing chronology we move from sensation to perception, by forming percepts that we experience phenomenally?

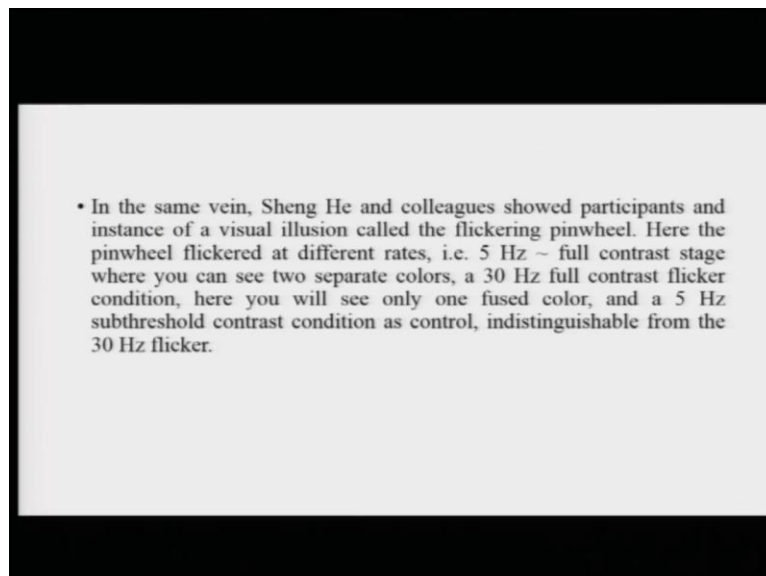
Now, we have talked about various aspects or various modalities of, various sensory modalities that allow us sensory information, which can then be processed to form percepts. We have talked in the beginning of this chapter that sensation and perception are slightly different concepts. And why one may lead to the other, the exact mechanisms and the relationship between sensation and perception is something that is a subject of debate. One of the questions that neuroscientists have wondered about, is about at which stage the visual processing, at which stage of the visual processing chronology we moved from the just sensory information to forming whole coherent percepts.

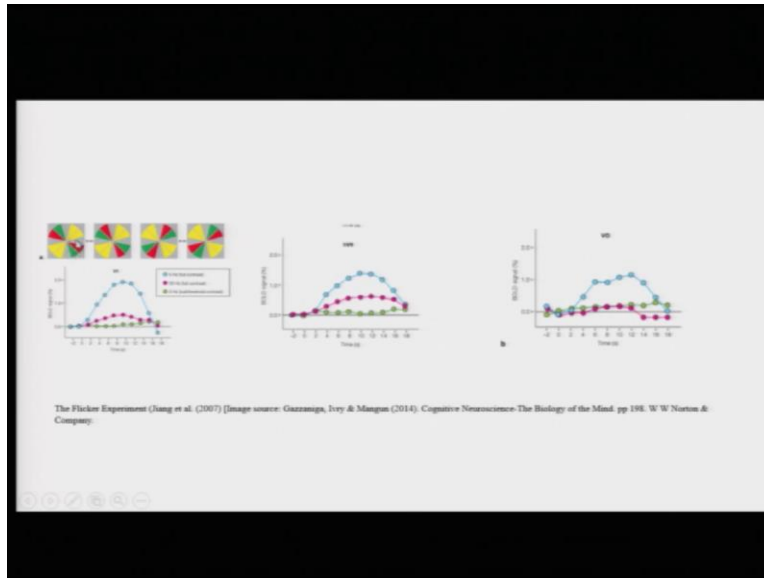
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Interesting insights about the following question can actually be gained from scenarios where the so called perceptual experience turns out to be slightly different from the sensory information that is being gained by the senses. If we follow the neural processing of such stimuli using available techniques such as PET, fMRI, DTI whatever, we may be able to uncover the stage at which the divergence between sensory processing and perceptual processing can happen.

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Let us take an example. In the same vein, Sheng He and colleagues showed participants an instance of a visual illusion called the, which involves the flickering pinwheel. It is called flicker fusion. Basically, what happens is that you will see this kind of a pinwheel, which with different colors and this pinwheel could flicker at different speeds. At higher speeds, it would basically give you a combination of the colors that are involved in the pinwheel. So, this is therefore called a flickering fusion.

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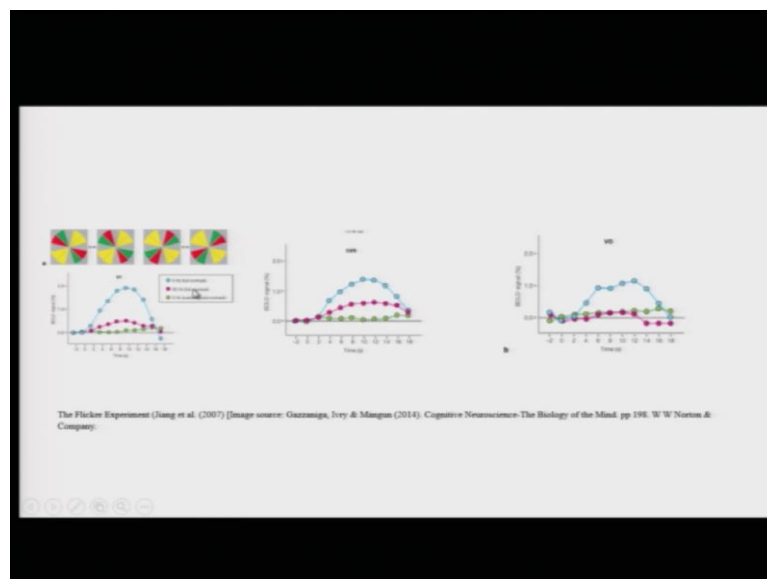
- In the same vein, Sheng He and colleagues showed participants and instance of a visual illusion called the flickering pinwheel. Here the pinwheel flickered at different rates, i.e. 5 Hz ~ full contrast stage where you can see two separate colors, a 30 Hz full contrast flicker condition, here you will see only one fused color, and a 5 Hz subthreshold contrast condition as control, indistinguishable from the 30 Hz flicker.

Now, here in their experiment, the pinwheel flickered at three different rates, at 5 hertz, where you can see the full contrast, where you can see two separate colors, at 30 hertz rate where the full contrast flicker condition, where you will see just one fused color and a 5 hertz subthreshold contrast condition, which is basically static and indistinguishable from the 30 hertz flickering

condition. So, both the 30 hertz flickering condition and the 5 hertz control condition are sort of indistinguishable from each other.

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- It was observed that while subcortical several lower cortical processing areas such as V1 & V4, could distinguish between the 3 flicker conditions; the BOLD response from VO, an area adjacent to V4 could not differentiate between the high-flickering and the static stimulus.
- It could be concluded that the percept that we see – of a non-flickering yellowish object – is formed in the area VO. This would imply that while sensory information is accurately processed at earlier regions of the visual stream, the resultant visual illusion is formed at a slightly higher cortical area.



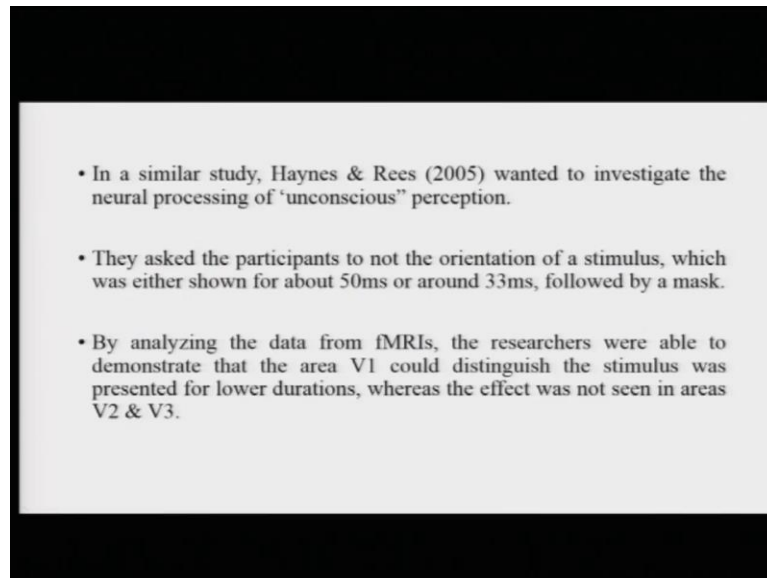
It was observed that while the subcortical, while say basically the subcortical and several lower cortical processing areas such as the V1 and V4 could distinguish between the three flicker conditions. The BOLD response from an area called the ventral occipital adjacent, which is adjacent to the area V4 could not distinguish between the high flickering and the static stimulus.

It could therefore be concluded that the perception that we see of non-flickering yellowish object which is formed from the fusion of these colors is actually formed at the area VO. This basically implies that while sensory information is more accurately processed at earlier regions

of the visual stream, the resultant visual illusion may be formed at higher cortical areas where the information is being integrated.

This is the example, you can see the responses from the area V4 and you can see the responses from the area VO here, where you can see that the distinction between the 30 hertz flicker and the 5 hertz control condition is almost absent.

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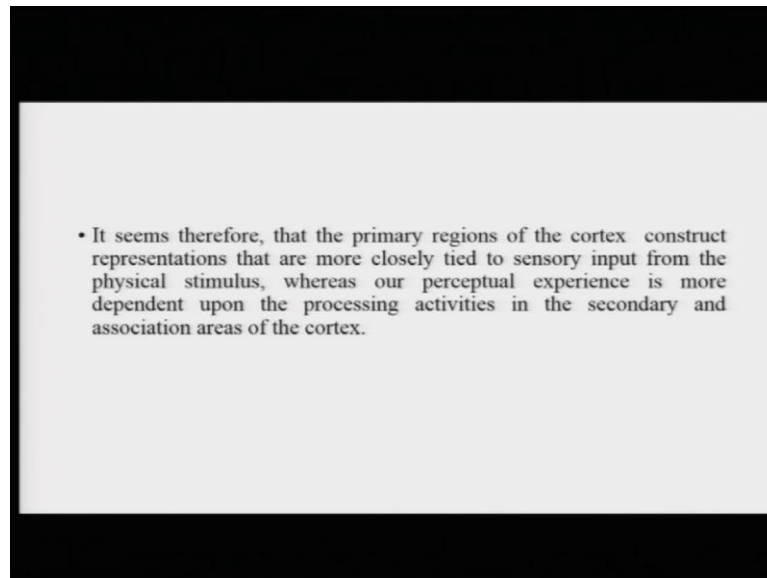


In a similar study, Haynes & Rees in 2005 wanted to investigate the neural processing of what is called unconscious perception. Typically, when you present stimuli under a particular threshold, you are not able to consciously perceive those stimuli. So this is basically what Haynes and Rees wanted to really check out.

They asked the participants to note the orientation of a stimulus, which was either shown for just around 50 milliseconds, or even lower than the threshold at around 33 milliseconds. And then, the same should be followed by a mask and the participants would sort of, will need to decide whether or what the orientation on the stimuli was.

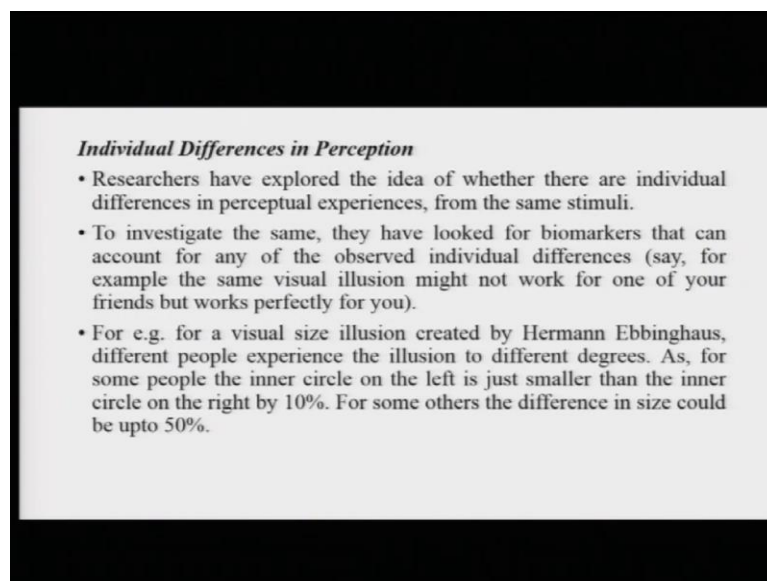
By analyzing the data from fMRI technique, these researchers were able to demonstrate that the area V1 could distinguish, could actually distinguish the stimulus when it was presented for lower durations, whereas this effect was not seen in areas V2 and V3, basically telling us that the primary regions of the cortex construct sensory representations which are closely or construct representations which are more closely tied to the sensory input from the physical stimulus.

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But with the higher areas or higher cortical areas are where our perceptual experience is more dependent upon the processing activities in the secondary and association area. So they need a degree of conscious processing.

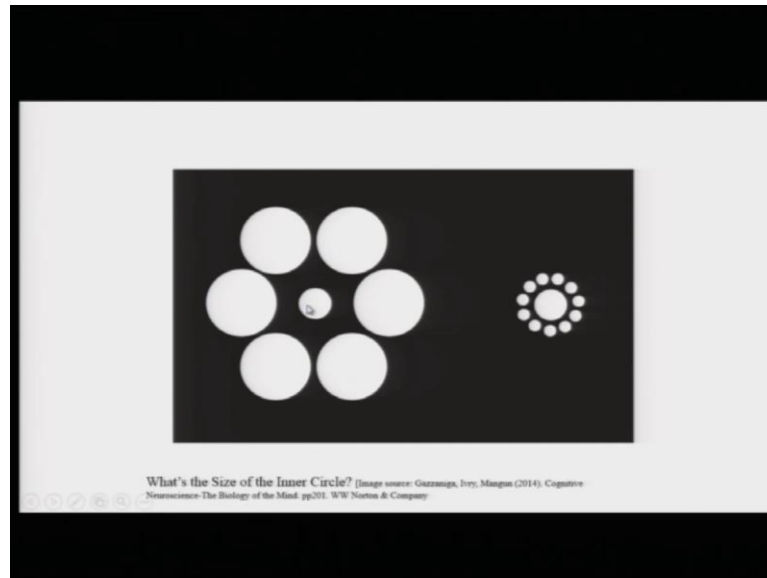
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Now, there are several individual differences that have been observed in perception, not only visual but of other kinds as well. Researchers have explored the idea of whether there are these same kind of stimuli and what are the biomarkers that can actually explain the difference in perception between individuals. Now, the same researchers have looked for biomarkers which can account for the observed individual differences. Say for example, the same visual illusion

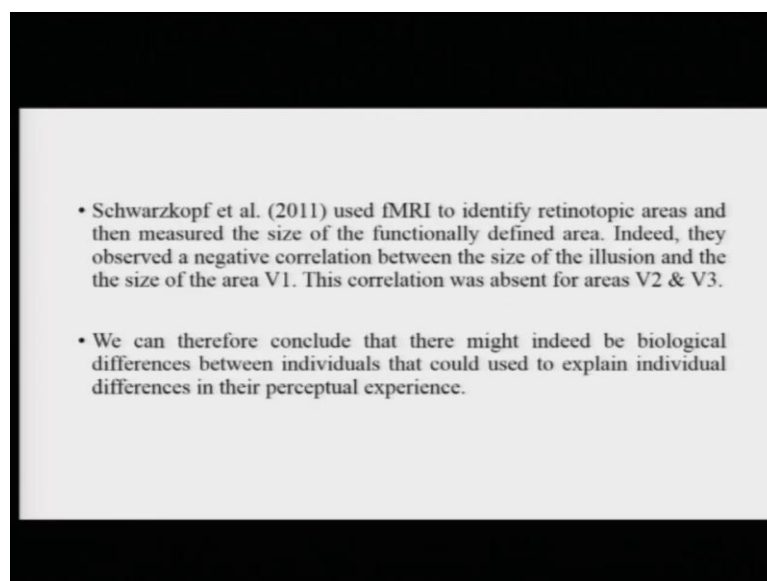
might actually not work for you, you cannot see the illusion happening. But one of your friend is just going, is just going crazy about it because for him or her the illusion is actually working.

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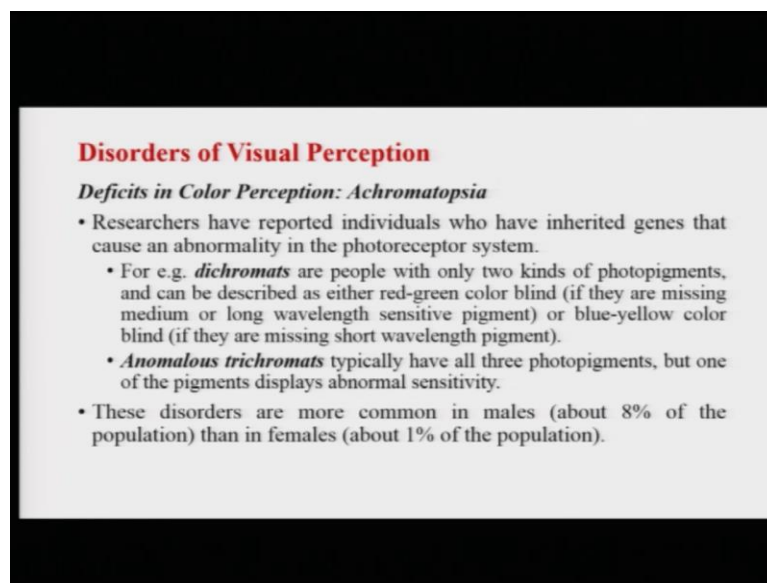
Let us take an example of such a visual illusion. If you look at the two pictures here, I am sure you would know that the size of the central circle in both the cases is the same. But for some people, this circle would appear larger than this circle by 10 percent. For some others, this circle would feel larger by this circle by almost 50 percent. Now, this individual variation in the perception of the difference of size between the two identical stimuli is something that people have wanted to figure out.

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Now Schwarzkopf and colleagues in 2011 used fMRI to identify the retinotopic areas and then measured the size of the functionally defined area, while participants were viewing this illusion. Indeed, they observed a negative correlation between the size of the illusion, let us say 10 percent or 50 percent or 40 percent, and the size of the area V1 in these individuals. This correlation was absent for areas V2 and V3. We can therefore conclude that there might be some kind of a biological underpinning, some kind of biological differences in the way individuals process the sensory input. And that is one of the things that is, that can be used to explain these individual differences in their perceptual experience.

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Disorders of Visual Perception

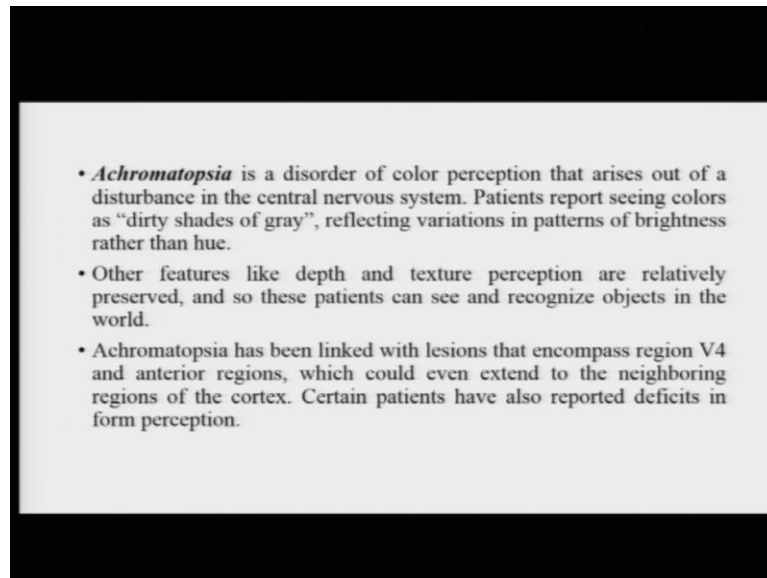
Deficits in Color Perception: Achromatopsia

- Researchers have reported individuals who have inherited genes that cause an abnormality in the photoreceptor system.
 - For e.g. *dichromats* are people with only two kinds of photopigments, and can be described as either red-green color blind (if they are missing medium or long wavelength sensitive pigment) or blue-yellow color blind (if they are missing short wavelength pigment).
 - *Anomalous trichromats* typically have all three photopigments, but one of the pigments displays abnormal sensitivity.
- These disorders are more common in males (about 8% of the population) than in females (about 1% of the population).

Let us move further onto disorders of visual perception. Now, disorders of visual perception can be of various kinds. One of them, some of them focus on deficits in color perception, deficits in color perception typically is referred to as achromatopsia, where you are not basically being able to perceive achromatic or you paste information. Now, researchers have reported individuals who have inherited genes that cause an abnormality in the photoreceptor system. Say for example, dichromats are people with only two kinds of photopigments. And therefore, they can be described as either red-green color blind, if they are missing the medium or long wavelength pigment or blue-yellow color blind if they are basically missing the short wavelength pigment.

Anomalous trichromats are people who typically have all three photopigments present. But one of the photopigments displays abnormal sensitivity and hence the coloration of these people is not normal. Similarly, these disorders are more, are found to be more common in males, more like about 88 percent than in females which is just about 1 percent of the population.

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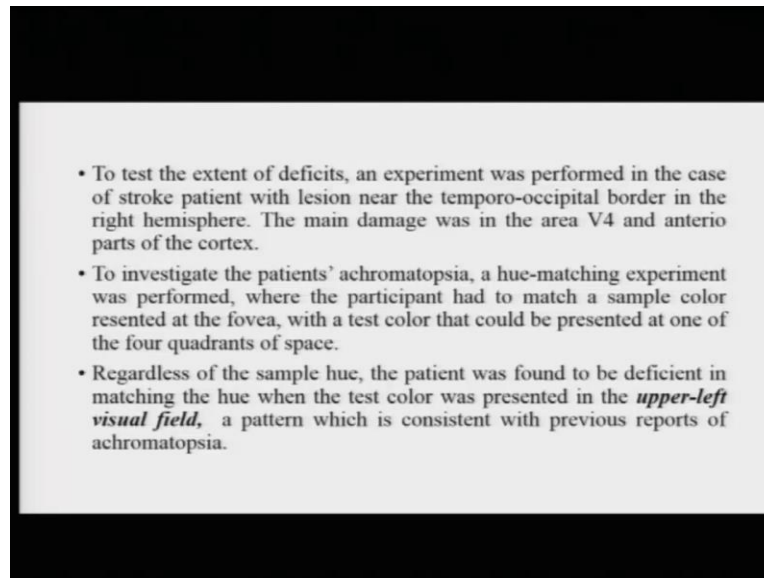


Now, achromatopsia is actually a disorder of color perception that arises out of a disturbance in the central nervous system. Patients report seeing colors as patches of gray as dirty shades of gray, reflecting variations in brightness rather than hue information or color information. Other features like the perception of depth and perception of texture are relatively preserved in these individuals, so that these patients can see and recognize objects in the environment.

Now, achromatopsia patients, achromatopsia per say has been linked with lesions that encompass the region V4 and slightly anterior regions to V4, which could basically then extend to other, to some of the neighboring regions of the cortex. Certain patients have also reported deficits in form perception.

If you remember, we just saw an experiment in the last lecture done by Zeki and colleagues where he, where they basically determined area V4 as the area which is responsible for color perception. So then, this is intuitively and this is intuitive as expected. But certain patients who have achromatopsia also report deficits in shape perception or form perception.

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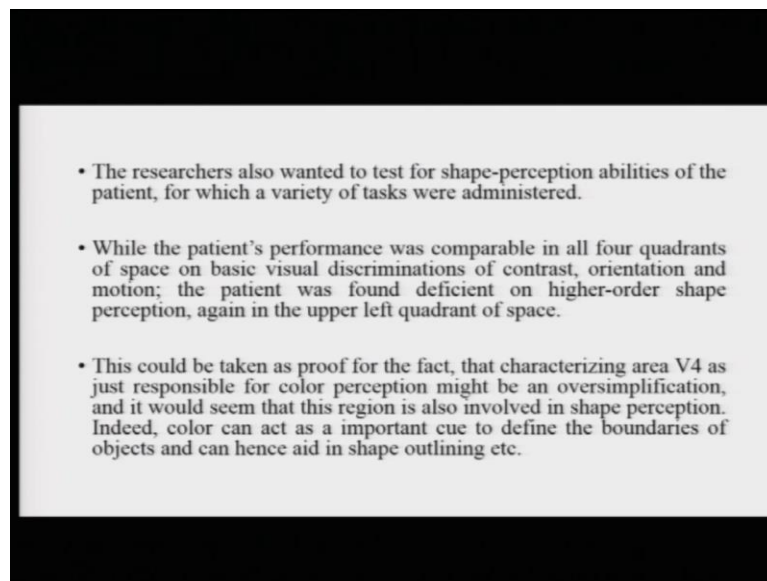


To test the extent of the shape perception deficits in these individuals, an experiment was performed. A patient was taken who had a stroke and had a lesion near the temporal occipital border in the right hemisphere. The main damage, however, was centered around the area before and the anterior parts of the cortex. To investigate the patient's achromatopsia, a color matching or a hue matching experiment was performed, where participants had to match a sample color which was presented at the fovea with a test color that could be presented in one of the four quadrants of space.

So you see something at the center. Let us say this is red color, and then in four quadrants of the straight left, right, and in the four quadrants of the space, you could, you will see another color that you will have to see whether it matches with the color that was centrally presented.

Now, regardless of whichever sample was chosen, the patient was actually found to be deficient matching the hue when the test color was presented in the upper left quadrant of the visual field. A pattern which is consistent with previous reports of achromatopsia. So this is basically the region where (achromatop), where patients of achromatopsia will face these deficits.

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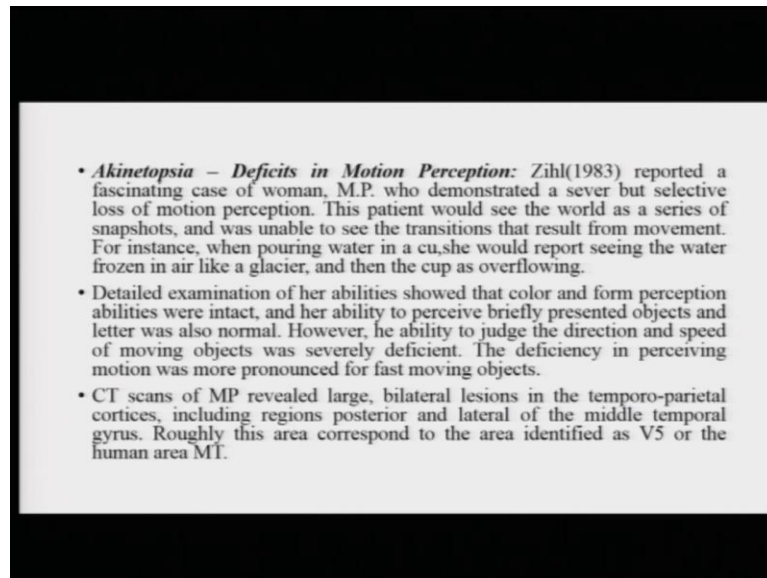


Now these researchers also wanted to test for shape perception abilities of the patient. And for that variety of tasks were administered. While the patient's performance was comparable for in all four quadrants of space for shape perception, and they were sort of in the normal range with respect to basic visual discriminations like contrast differences, orientation differences and motion differences, the patient was found to be deficient on higher order shape perception, again in the upper left quadrant of space.

Now, this sort of, can be taken as a proof for the fact that if we simply characterize the area V4 as only responsible for color perception, we might be committing a bit of a mistake. It would seem that this region is also involved in shape perception. Again, color can act as a very important cue for people and which can help people determine the shape of the objects just by differentiating between, say, for example, edges and other aspects of the object and help them in outlining the shape etc.

So, achromatopsia may also be linked with a certain degree of deficiency or certain degree of deficits in shape perception.

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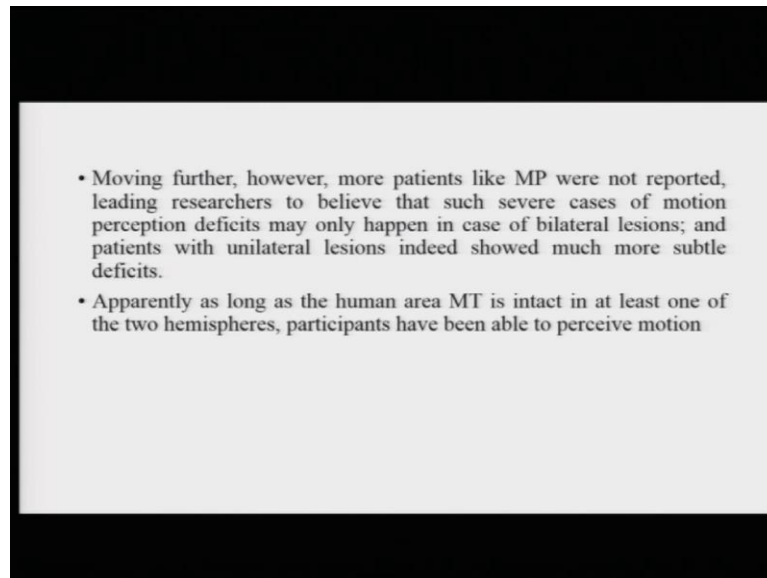


Now, another kind of deficit or another kind of problem of visual perception can be this deficit in perceiving motion. Patients who have deficits in pursuing motion can be characterized as having what is called akinetopsia. Zihl in 1983 reported a fascinating case of a woman called M.P., we call M.P. who demonstrated a severe but selective loss of motion perception. This patient would report seeing the world as a series of snapshots. Suppose if you are watching a movie, and the movie starts coming in series, one frame, then the other frame, then the other frame. This is typically what this patient was experiencing. She was unable to see the transitions that result from movement.

For instance, she would describe that when she is pouring water in a cup, she would report seeing the water frozen in the air like a glacier and then suddenly, the picture of a cup overflowing. Now detailed examination of the abilities of this particular patient, a detailed examination of the abilities of this particular patient showed that color perception and form perception abilities were fairly intact and her ability to perceive represented objects and letters was also normal.

However, her ability to judge the direction and motion of moving objects was severely deficient. The deficiency in perceiving motion was actually much more pronounced from objects that were moving fast. Now, CT scans of this patient M.P. revealed large bilateral lesions in the temporo-parietal cortices, including lesions posterior and lateral of the middle temporal gyrus. Roughly this area basically corresponds to the area V5 as identified as the human area VD, if you remember in the Zeki experiment in the last lecture.

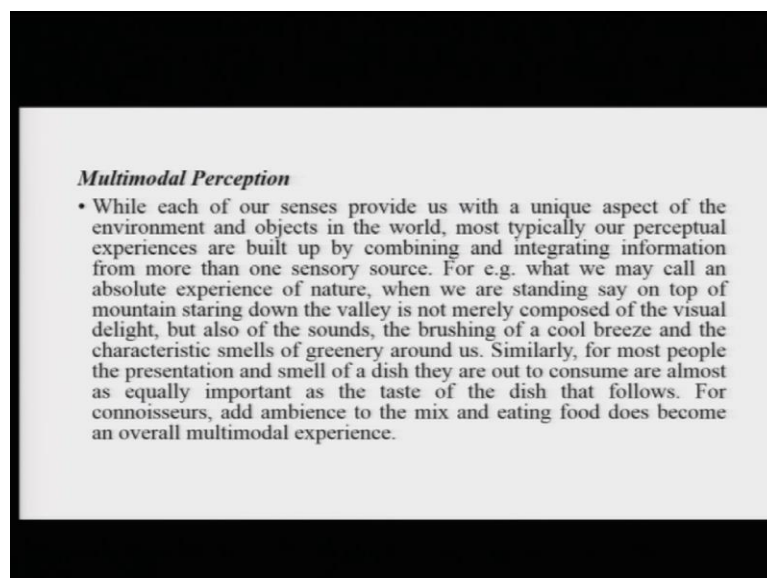
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Now moving further, however, I mean more patients like MP were not reported, but it sort of led the researchers to conclude that severe, such severe cases of motion perception deficits could only happen if the lesions are present in both the hemispheres of the individuals.

Typically, patients which have unilateral lesions in the human area VT, human area MT or area V5, basically showed much subtle deficits. So as long as one of the hemispheres, now, the area V5 is normal, patients will typically not really report severe problems with perceiving motion.

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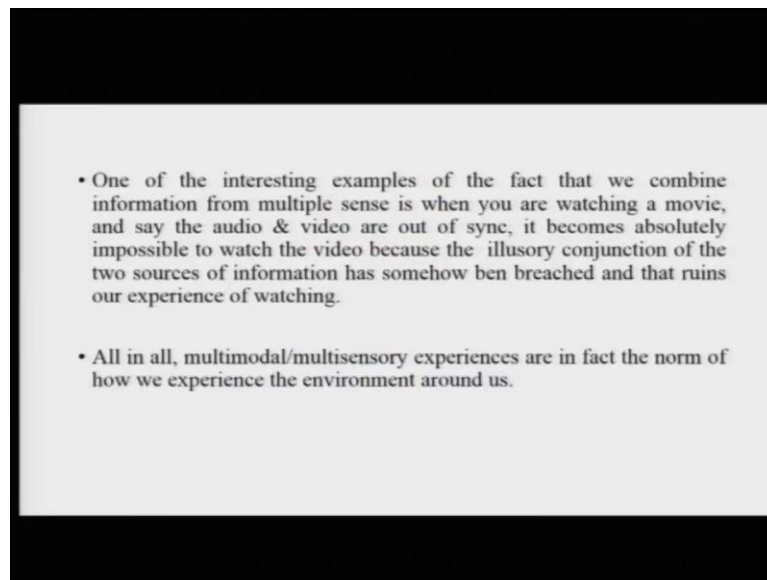
Now, while each of our senses provides us with a unique aspect of, provides us with a unique aspect of the environment and objects in the world, most typically, our perceptual experiences are built up by combining and integrating information from more than one sensory source. For

example, what we may call an absolute experience of nature. Now, suppose you are at a hill station, you are standing across the hill, you are looking down into the valley, which is basically more initially you will look at it as merely a visual delight, is actually a holistic experience, that is not only composed of the scenery, but it is also composed of sounds, of the smells, of the cool breeze that is brushing against your body.

And so, basically a perceptual exposure is actually a combination of all of these factors coming together. So similarly, we can take another example, say for example, for most people, the presentation and the smell of a particular dish that they are going to consume is actually equally as important as the taste of the dish. Because as you see, the appearance of the dish sort of precedes or the smell of the dish precedes the taste of the dish.

If say for example, you do not like the presentation of some dish, you will already lower your expectations as per the taste, you will already say for example sometimes....So in this sense, I am just giving you these examples to make you appreciate that information from multiple senses are sort of very, very important and sort of need to be combined together to give you an actual perceptual experience.

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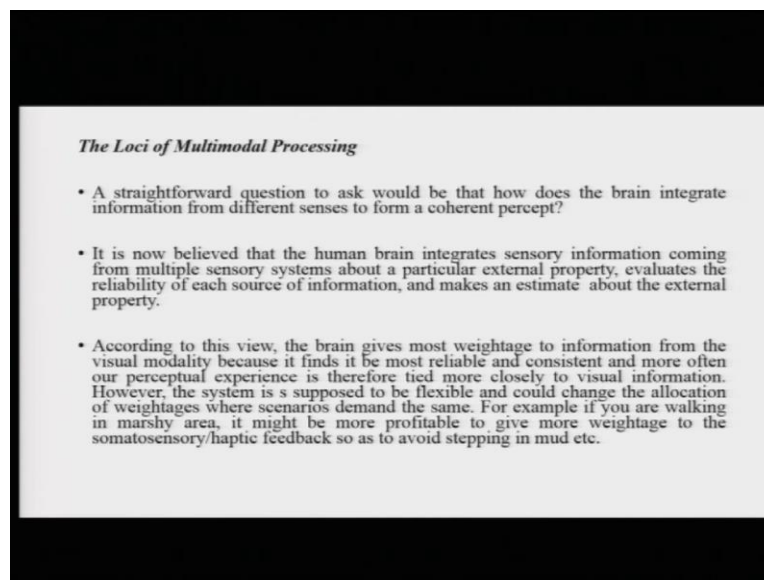
One of the interesting examples of the fact that we combine information from multiple senses, or multiple sensory modality, say, for example, when you are watching a movie and audio and the video of the movie are out of sync. It would become absolutely impossible. It would become absolutely impossible to watch the movie, because the illusory conjunction, conjunction of audio and video is basically breached.

We know say for example, otherwise that you know the audio is just being, the video is being placed at a high frame rate per second, video is basically, the audio is just pasted upon the video. So we know that this is actually a conjunction, but it almost appears that the characters in the movie are speaking those dialogues.

Once this link is breached, it becomes absolutely impossible to watch the movie. It ruins your experience of watching. So just looking at all three of these examples together, what we can conclude is that multimodal, or multi-sensory experiences are in fact the norm of how we experience the environment around us.

Even though for means of convenience, we have sort of studied them separately in this chapter. We can sort of, let us talk a little bit about how the information from these different senses are combined together to give you a more, a richer and a better perceptual experience.

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Now, let us talk about the loci of multimodal processing. Where does this actually happen in the brain? Now a straightforward question to ask would be that, how does the brain integrate information from different senses to form a coherent percept?

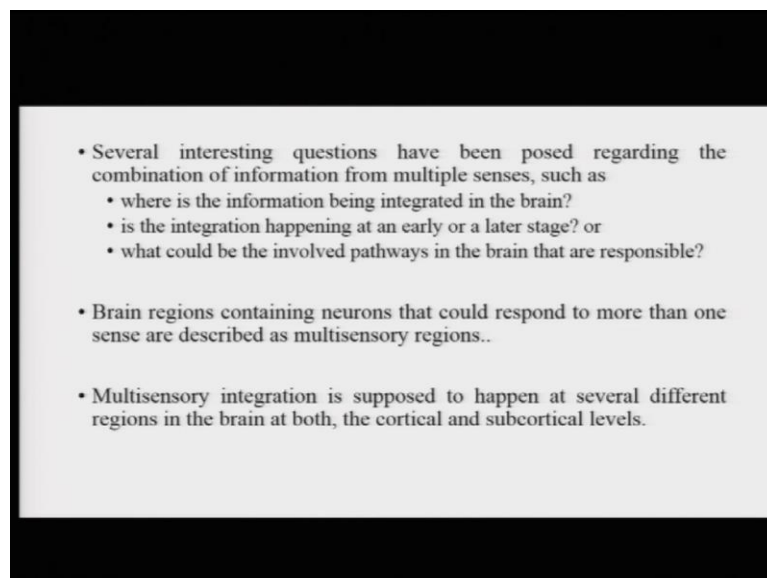
It is now believed that the human brain integrates sensory information coming from multiple sensory systems about an external property. And it evaluates the reliability of the, each of these sources of information, and then makes an estimate about this external property. Suppose you say, for example, navigating a particular area of marshy land, it would be therefore more probable to sort of and it will be more beneficial to you, if you are combining whatever you have seen visually with also the feedback from your feet, the happening feedback.

Because it will tell you whether it is safer to tread further on that ground or not. Because sometimes you might run into muddy areas or say for example, quicksand or something like that.

So, typically, in such a scenario, it would happen is that, say for example, while the brain most typically gives most weightage to the visual modality, it might say, for example, try and reorganize its system and start relying a little bit more on the haptic feedback. Typically, it is reported that say for example, the brain gives more weightage to the visual modality. And this is probably also one of the reasons why most of our interactions are predominantly decided by the information that is coming from the visual sense. But obviously, there can be different circumstances, just like the one I explained, where it becomes slightly more important to give more weightage to the other kind of information.

You can say for example, the same would be true for areas where the visibility is slightly lower. So you have to kind of rely on your auditory information to navigate the path or say for example, to look for, if you are gone hunting to look for, those kind of things.

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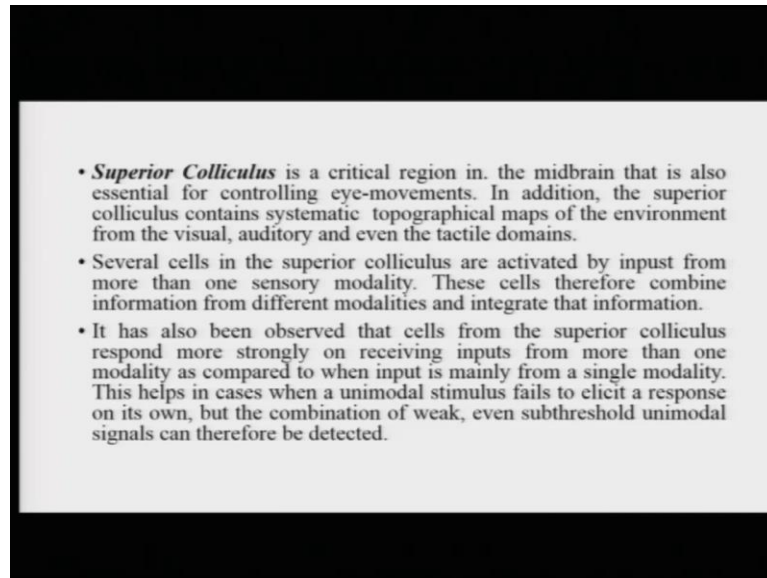


Now, several interesting questions have been posed regarding the combination of information from multiple senses, such as say for example, where is this information being integrated in the brain? Is the integration happening at early stage or a later stage? Or say for example, what are the involved pathways in the brain that are making this possible?

Brain regions have been known to contain neurons that could respond to more than one senses. And these regions are supposed to be called multisensory or multisensory regions of the brain.

Multisensory integration is actually supposed to happen at several different regions of the brain, both at the cortical and the subcortical levels.

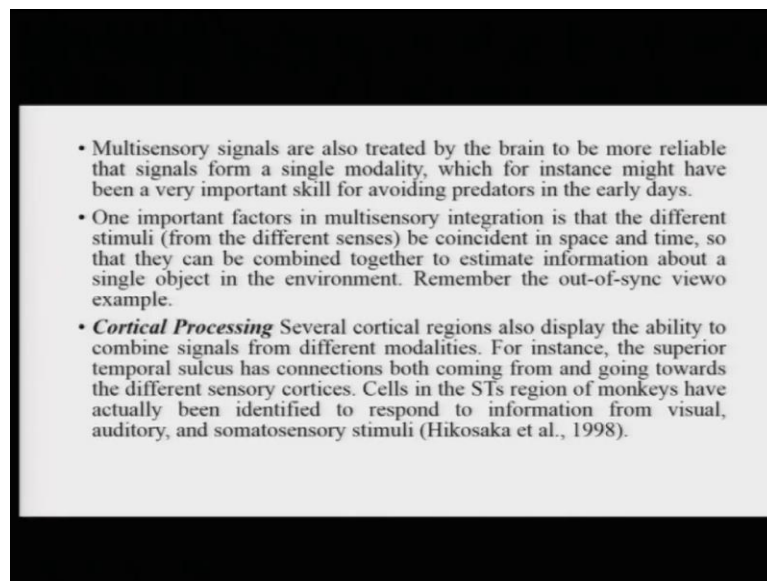
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Let us take an example of subcortical region in the superior colliculus. You might know, I mean, I am sure you know, superior colliculus is a critical region in the midbrain that is also essentially for controlling eye movements. In addition, the superior colliculus contains systematic topographical maps of the environment based on visual, auditory and even tactile information. Several cells in the superior colliculus are activated by inputs from more than one sensory modality. These cells can combine information from different modalities and integrate that information to give you a holistic percept.

It has also been observed that cells from the superior colliculus respond more strongly on receiving inputs from more than one modality. And they respond slightly weakly if the input is just coming from one of these modalities. This can actually help us detect particular stimuli when just unimodal simulation or unimodal signals from that stimuli fail to activate, thus fail to activate the system.

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Now multisensory signals are also trained by the brain to be more reliable, are also treated by the brain as more reliable than signals merely from a single modality. Which for instance, might have been a very important skill for say, for example, avoiding predators in early days. Say for example, you will see something and you are also listening and you are also, say for example, you know, depending upon your, upon the haptic feedback if you are kind of navigating through an area of jungle where you need to avoid predators.

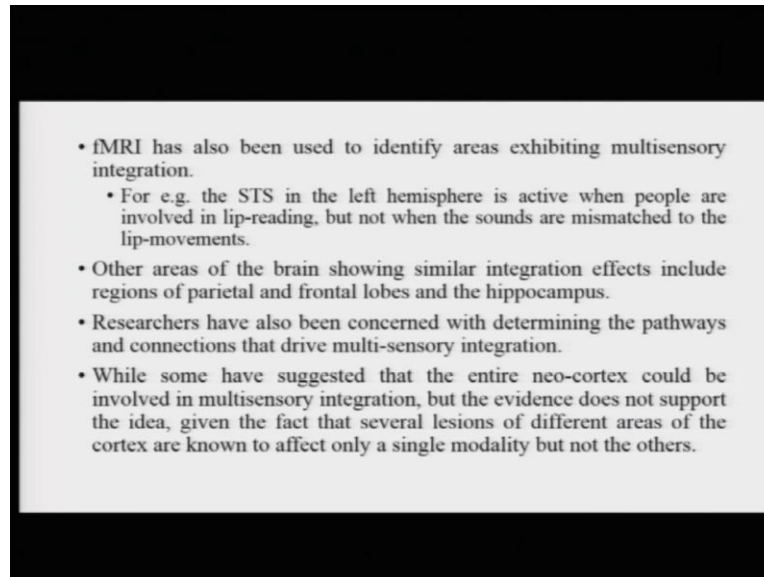
Now, one of the very important factors in multisensory integration is that different stimuli from or different kinds of information or different stimulation from these different sensory modalities need to be coincidental in space and time. So all the information should be arriving at the same time from the same region of space.

That is what would help the cells in these multisensory regions to combine those informations, to tie them together and to give you a sort of a combined percept. Remember the example that I just gave of out of sync videos. If you are seeing out of sync videos, you will not be able to say for example, because there is this temporal gap between how the video is moving and where, how the audio is coming, it becomes completely incomprehensible and very difficult to watch those features.

Now, let us talk about areas in the cortex that might be responsible for multisensory integration. Several regions of the cortex are display this ability to combine signal from different modalities. For example, the superior temporal sulcus has connections both coming from and going towards the different sensory cortices. It provides us with a unique opportunity of combining those signals together.

Cells in this superior temporal sulcus region of monkeys have actually been identified to respond to information coming from visual, auditory and somatosensory stimuli. So in that sense, there is already evidence of the fact that the superior temporal sulcus in the humans might also be doing it.

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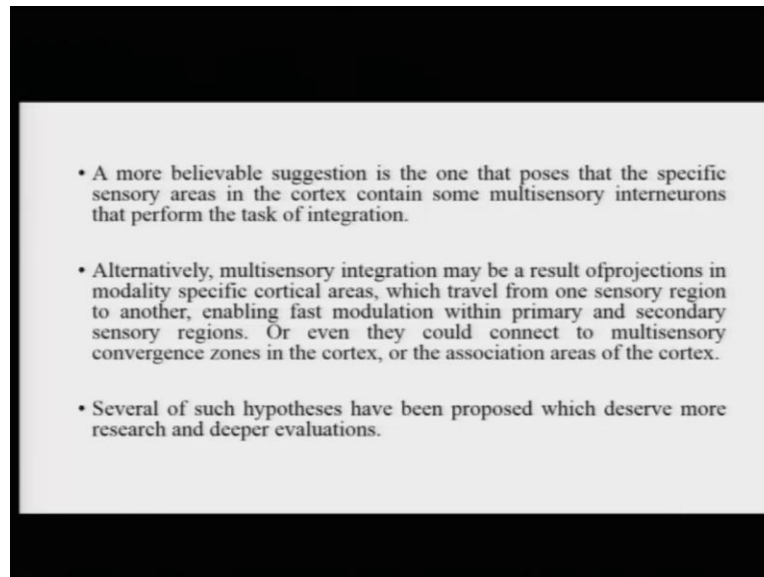
fMRI has actually been used to identify the area exhibiting multisensory integration in the human cerebral cortex. For example, the superior temporal sulcus in the left hemisphere is found to be active when people are actively engaged in lip reading, when they are actually, say for example, observing how the lips of another person are going while they are speaking.

But the same region is not found to be activated when the sounds are mismatched for the lip movements. So typically saying that maybe when there is no possibility of integration, then the region is not active. Or say, for example, yeah, the region is not invoked when the requirement is not as such. Now, other areas of the brain which show, also shows similar integration effects include the regions of parietal and frontal lobes and also the hippocampus.

Researchers have also been concerned with determining pathways and connections that actually drive these multisensory integrations. Now, some people have suggested that it is probably the entire neo-cortex that could be involved in multisensory integration. But then that is probably an exaggeration, because there is a lot of evidence that suggests that people have lesions in specific areas of the cortex. And those specific lesions actually lead to do deficiencies in only very specific, only very specific sensory modalities.

Say for example, people who suffer from lesions in the extra striate cortex might suffer from deficiencies like visual agnosia, but their hearing and other kinds of capabilities might be unaffected. So this could be a little bit of exaggeration.

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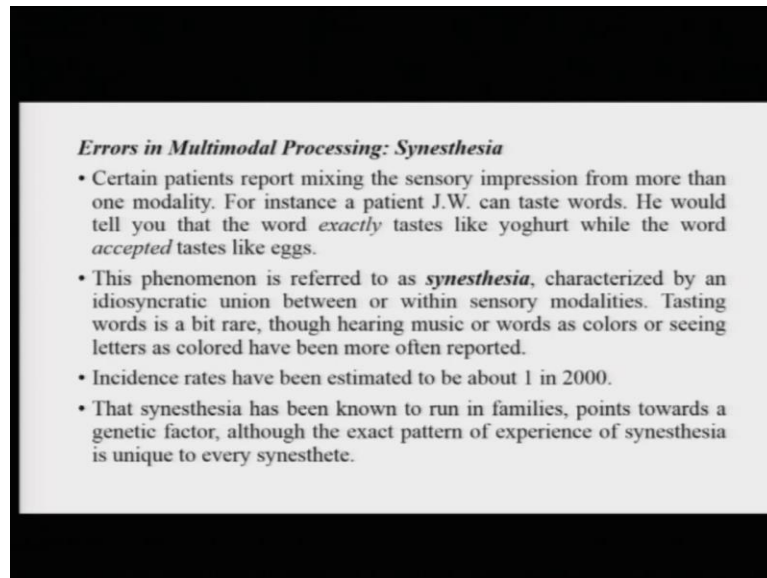


But let us say a more believable suggestion could be that, say for example, specific sensitive areas in the cortex contain what are called multi-sensory interneurons that actually are performing the task of integration. Another possibility could be that multisensory integration could be a result of projections in modalities specific cortical areas which travel from one sensory region to the other, and basically enable fast modulation within primary and secondary cortices or primary and secondary sensory processing areas.

Even say, for example, they could connect multisensory convergence zones in the cortex, or as they are called association areas of the cortex. So, probably, these are the reasons where you know, all of this integration of sensory information is happening.

Now, several such hypotheses have actually been proposed, which sort of deserve a more research and more deeper evaluations before we can actually figure something about how exactly this multisensory integration or forming of this holistic process actually takes place in the brain.

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Errors in Multimodal Processing: Synesthesia

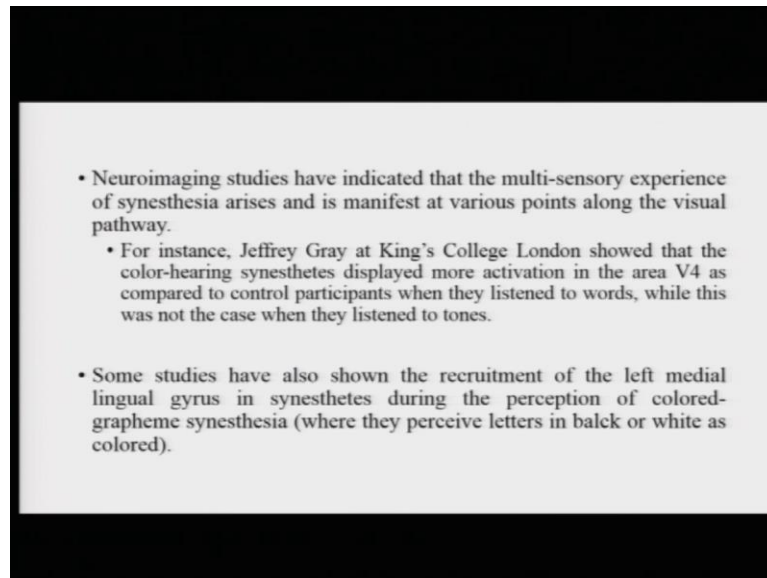
- Certain patients report mixing the sensory impression from more than one modality. For instance a patient J.W. can taste words. He would tell you that the word *exactly* tastes like yoghurt while the word *accepted* tastes like eggs.
- This phenomenon is referred to as *synesthesia*, characterized by an idiosyncratic union between or within sensory modalities. Tasting words is a bit rare, though hearing music or words as colors or seeing letters as colored have been more often reported.
- Incidence rates have been estimated to be about 1 in 2000.
- That synesthesia has been known to run in families, points towards a genetic factor, although the exact pattern of experience of synesthesia is unique to every synesthete.

Now, let us talk a little bit about, say for example, possibilities of errors in multimodal processing. Certain patients fascinatingly report mixing sensory impressions from more than one modality. For example, a patient JW reports that he can taste words. He would tell you that a word exactly tastes like, whereas the word accepted tastes like eggs.

This is slightly fascinating. And this particular phenomena is referred to as synesthesia. Synesthesia is characterized by an idiosyncratic union between or within sensory modalities. Why do I call it idiosyncratic is because the pattern of this union or the pattern of combinations of these senses are unique for most patients, words is a little bit today. But say for example, a lot of people report hearing music or words as colors, or seeing letters as colored, more often than not.

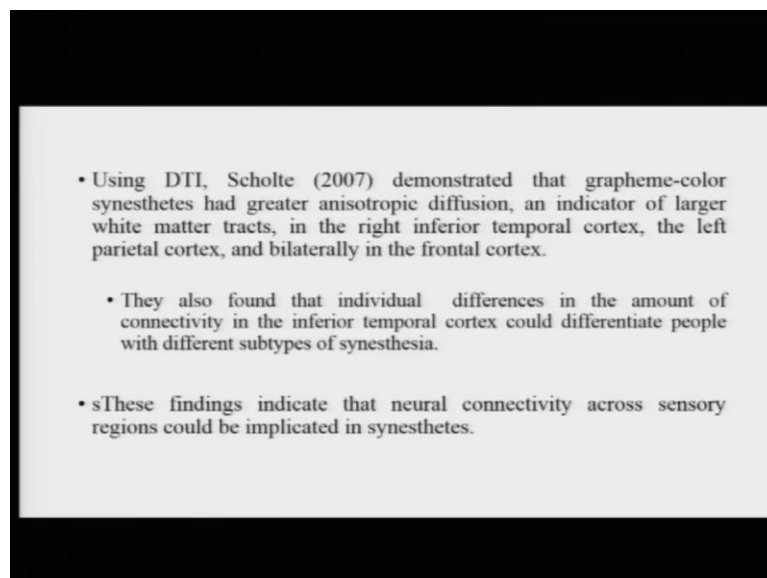
Incidence rates of synesthesia has been estimated to be around 1 in 2000, which tells us that it is a little bit rare. And also, the fact that synesthesia has been reported to run in families tells us or it points towards sort of a genetic factor individuals that have synesthesia.

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Now, neuroimaging studies have basically indicated that multisensory experience in synesthesia arises and this manifests at several levels or various points in the visual processing pathways. For instance, Jeffrey Gray at King's College London showed that color-hearing synesthetes, the ones who hear words as colors are displayed more activation in the area V4 as compared to control participants when they listen to the same words. This activation was absent when these synesthetes were hearing or listening to tones as opposed to these words. Some studies have also shown that they have also sort of reported the recruitment of left medial lingual gyrus in synesthetes during the perception of color grapheme synesthesia where they see letters written in black and white as colored.

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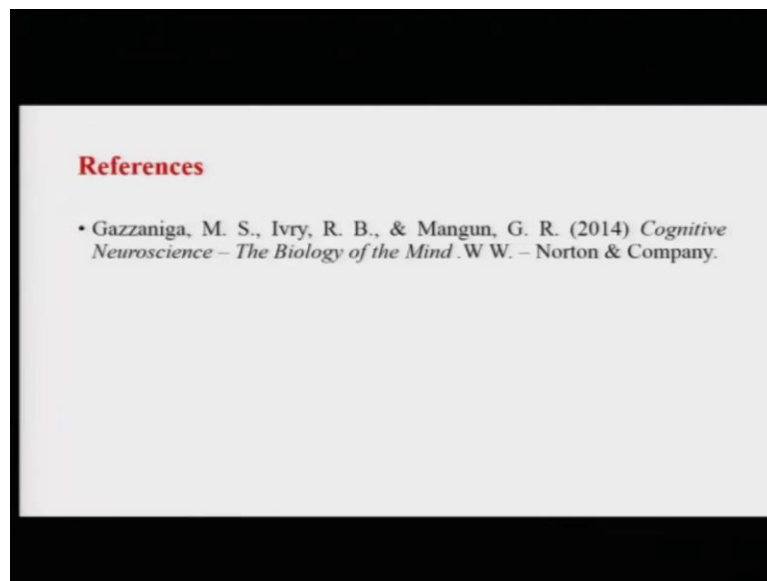


Now, using DTI, diffusion tensor imaging that is, Scholte in 2007 has demonstrated that grapheme-color synesthetes those that see letters as colored had greater anisotropic diffusion, which is a marker of larger white matter tracts, more interconnections between different regions of the brain in the right temporal cortex, the left parietal cortex and bilaterally in the frontal cortices.

This basically they also found individual differences in the amount of connectivity in, they also found that individual differences and the amount of connectivity in the inferior temporal cortex could actually differentiate between people having different subtypes of synesthesia.

So, these findings together, basically, they can actually tell us that neural activity across sensory regions could actually be, neural connectivity across sensory regions can actually be implicated in patients with synesthesia. So it could be that, say for example, the connections, or the interconnections between different sensory regions are slightly different in people who experience synesthesia, as opposed to other people who do not experience synesthesia.

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So this is, I think all that I wanted to say about sensation and perception. I hope you understood some of the sections I have covered in this chapter. And in the next week, we will talk about some other aspect of cognitive neuroscience. Thank you.