Introduction to Biomolecules
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Lecture – 11
Enzymes (Part 5/5) And Carbohydrates (Part 1/2)

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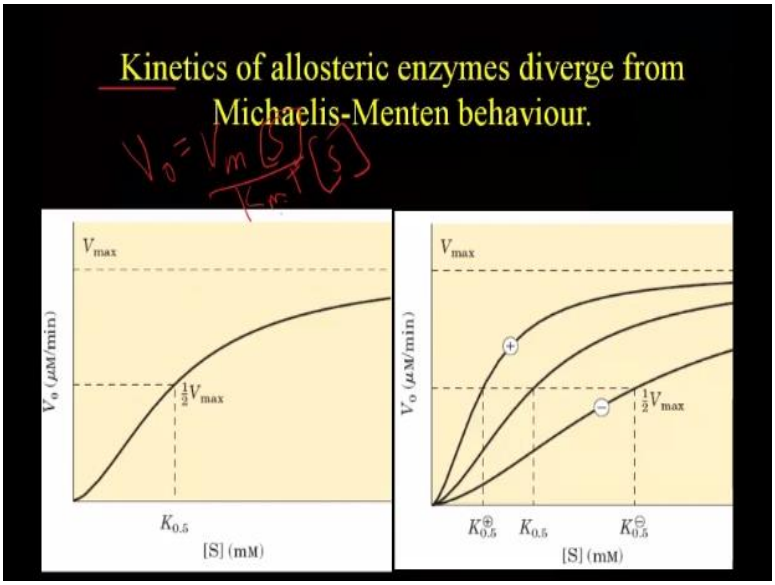

Okay so let us get started. So, in the last class we were discussing about allosteric enzymes and the very last thing was the feedback regulation of allosteric enzymes. In a biochemical pathway usually the enzyme catalyzing the committed step or the one of the earliest steps in the biosynthetic pathway is subject to feedback inhibition by the end product of that particular pathway.

So today we will briefly look at the kinetics of allosteric enzymes and then we will go into other ways of regulation of enzymes. So, since you have a positive cooperativity kind of situation where binding of substrate to one of the subunits, remember allosteric enzymes are usually multi-subunit enzymes. So that activates binding of substrates to the active sites of other subunits as well.

So as a result, the initial substrate binding leads to significant increase in the rate of the reaction because the binding to the other subunits is increased by this and as a result you get this sigmoidal shaped graph when you plot the rate of the reaction again substrate concentration. But still the saturation is the same, so therefore the half V max still remains the

same. And here since their behavior diverges from typical Michaelis-Menten equation where you have that saturation graph.

So, we do not call it as K m, instead that constant is called the K half okay. So that is the only main difference and this important change in the graph. So initially it is not linear okay. So in Michaelis-Menten enzyme it would have been linear because at the very initial stage the K m is we ignore the concentration of the substrate in the equation and as a result it becomes V max S by K m + S and when you ignore S, V max by K m remains constant.

So therefore, the velocity varies linearly with the substrate, right. So, in this equation like say we have so V 0 equals you have V max S divided by. So, in this equation very early we would ignore this, so then V max by K m remains constant, so V 0 equals substrate. So, it will be very linearly with substrate concentration. And that situation you do not see in allosteric enzymes because initial binding increases binding to the other subunits and as a result as it binds more it starts to increase after lag period okay.

So, this is characteristic shape of the curve for an allosteric enzyme. And when you have a positive interaction like positive cooperativity that is binding to one subunit enhances the binding to the other subunits as we see in oxygen binding to hemoglobin, then it shifts this direction. So, this is a with a positive regulation and with negative regulation it shifts in the opposite direction okay. So, these are characteristics of allosteric regulation.

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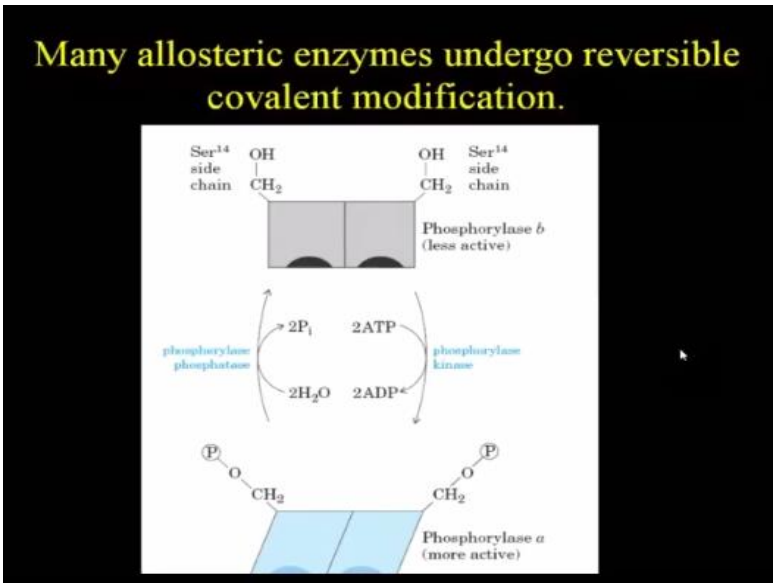

So that is all the kinetics we are going to learn because we are not going to become a enzymologist here, we are just getting a flavor for biochemistry, so this is just to have the basic idea. And many of these allosteric enzymes in addition to the binding of the molecules okay, the molecule that binds need not always be substrate, only in the case of hemoglobin it is substrate itself.

In other situations, I told you the end product of the pathway might regulate the upstream enzyme. So, in that case it is not the substrate, it is another molecule. So, it could be any molecule that binds to a catalytic site regulatory subunit modifies the overall conformation such that the active site in the catalytic subunit is affected. So, remember the R subunit, C subunit cartoon that you saw in the last class.

So, one of the other ways of regulation of these enzymes is covalent modification. So, one of the residues on the enzyme for example if this is an enzyme, so it has two subunits it is phosphorylase. So, this is involved in removal of phosphate groups and when in this case the 14 th serine it is hydroxyl group when it gets phosphorylated it becomes more active okay. So, in both the subunits you have two serene residues in two subunits and when both are phosphorus it is active.

And when the phosphate groups are removed by phosphorylase phosphatase, so the substrate is this enzyme phosphorylase and another enzyme phosphate is removed that phosphate group then it becomes inactive. So, by this way you can have a regulation through covalent modification. So, this phosphorylation is a very common modification of many enzymes, variety of enzymes not just phosphorylase itself.

So, this phosphorylation based regulation of enzyme activity when originally discovered people did not realize it is prevalence among very large number of proteins and later when it was realized this discovery was considered as a very profound conceptually advancing finding in biochemistry and scientists were awarded with Nobel prize for the discovery of phosphorylation as an important enzymatic regulatory mechanism.

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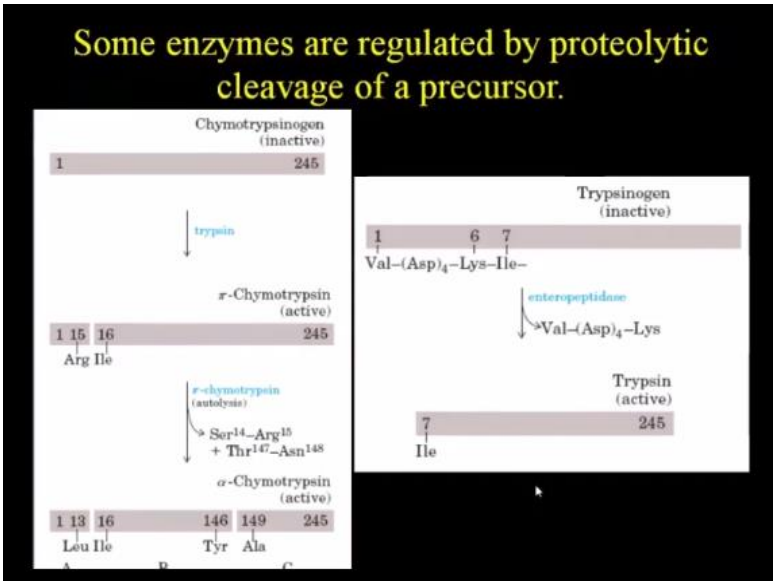

And another way of regulation is the enzymes are usually produced as a longer polypeptide than the active form. So, a part of the polypeptide usually the N-terminus gets proteolytically cleaved. For example, chymotrypsin is produced as chymotrypsinogen. So that precursor forms that are inactive are often named by this addition of gen, trypsin trypsinogen okay. And once it is cleaved by an active version of the same enzyme in this particular case.

So, you have like these 15 amino acids removed then you have further cleavages, then you have finally the active enzyme trypsin okay. So, in this case chymotrypsin and similarly trypsinogen becomes trypsin. And in this case, it is an enteropeptidase, entero referring to intestine okay, anything to do with the digestive system you call entero okay. That is why you call gastroenterologist, the doctor who specializes in digestion related issues.

So, trypsin activates chymotrypsinogen by cleaving between this arginine and isoleucine and then further cleavages by chymotrypsin itself resulting in the active enzyme okay, so this C-terminal portion. And similarly, trypsinogen gets cleaved as shown in this cartoon to become active trypsin. And this sort of proteolytic activity based activation is common in blood clotting pathway as well and similarly in complement pathway in our immune system.

And also in many of the peptide hormones they are activated again by proteolytic cleavage. So proteolytic cleavage based activation again is fairly widespread as a regulatory mechanism. Alright so this is all our discussion on enzymes. So, we got a basic idea of what are enzymes and how they achieve rate enhancement. The main point you want to remember

that is the various non-covalent interactions that happen that lead to distortion of the substrate reaching the transition state.

And the enzyme changing itself to fit to the transition state a phenomenon called induced fate okay. And the cumulative energy coming from all these non-covalent interactions we call binding energy, and this binding energy is the main component of reducing the activation energy. So, this is the main concept in enzymes that you need to remember. Then how we relate the rate of the enzymatic reaction.

Enzyme catalyzed reaction to the substrate concentration using Michaelis-Menten equation and its transformed version that is a double reciprocal plot. Then you need to remember how the enzyme activity gets affected with various kinds of inhibitors being present. Then the last main concept is the allosteric enzymes okay. So, if we know these basic concepts of enzymes then that is good enough for an introductory course in biochemistry.

So next we move on to our first major molecules that is called carbohydrates okay. So carbohydrates are the most abundant organic molecules on earth primarily because of their versatility in terms of use both as structural material like cellulose forms the major structural components, cellulose fibrils of the plant kingdom and the amount of plants on earth versus animals.

And cellulose itself can account for why carbohydrates are most abundant. In addition, they are very useful as storage of energy like the starch that we primarily depend on for our energy source is carbohydrate and the exoskeleton of insects, you would have seen many insects their wings are covered by a thick shiny outer cover okay and those shiny things are made up of a variety of polysaccharide called chitin okay, we will see soon.

So, this chitin and cellulose are extremely abundant. So, let us get into the basic structures. We already have familiarized ourselves with the terms like monosaccharides, polysaccharides, aldoses, ketoses and then glycosidic bond, etc. So, we will refresh our memory and get into more details today.

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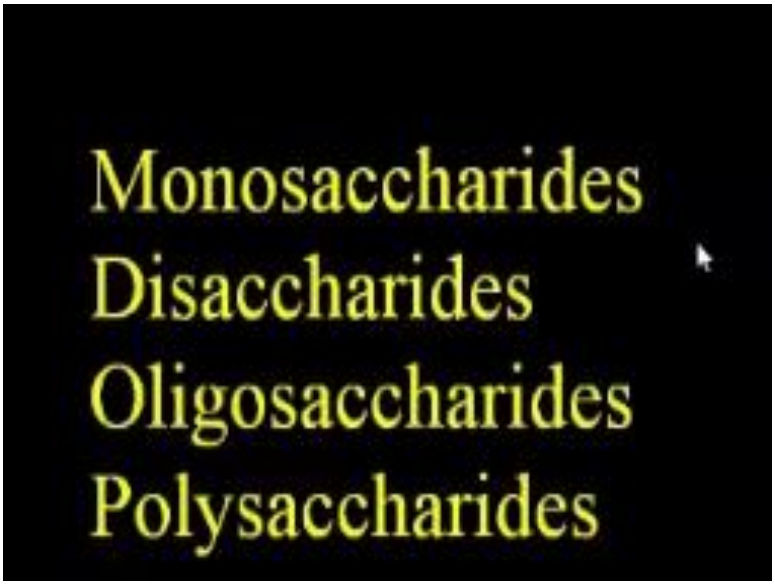

So, we know carbohydrates; the smallest units are the monosaccharides which are linked through glycosidic bonds to form disaccharides, oligosaccharides and then polysaccharides.

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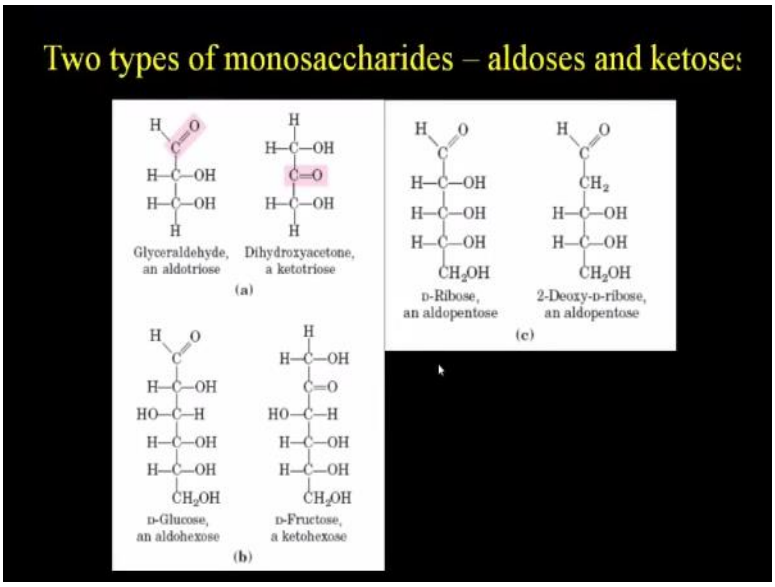

So first we will see monosaccharides. The smallest is glyceraldehyde which has an aldehyde group, so it is an aldose and it has 3 groups. So, there are 3 carbons so we call it as triose, so it is an aldotriose. And you may have instead a keto group dihydroxyacetone, so ketotriose. So, fructose which is the common ketos that you encounter like for example the common sugar that you add to coffee, tea or milk whatever it is a disaccharide.

One molecule is glucose another molecule is fructose. And fructose the name itself tells you is very abundant in fruits okay. Most fruits contain fructose usually about 4% of the fruits weight, but some dry fruits like for example dates can have way too much fructose to be

healthy. So as a result, eating dates too much of it is not good for health at all, you know completely contrary to TV advertisements that you frequently see.

So, the word fructose comes from fruit okay, it is rich in fruit. So, these two are the most common ones. Glucose you know starch breakdown product is glucose and fructose exist as a monosaccharide in fruits and in the common sugar these two exist as disaccharide. So, before we go further on to considering the various monosaccharides, let us focus our attention to the stereochemistry a little bit here.

So, if you look at glyceraldehyde structure, so this carbon is not chiral, it has two same group hydrogen attached. If you take this carbon one aldehyde group, one hydrogen and then an alcohol hydroxyl group, then you have this the CH 2 OH group this alcohol group methyl group attached here okay. And so as a result, these are 4 different substituents and as a result this is a chiral carbon.

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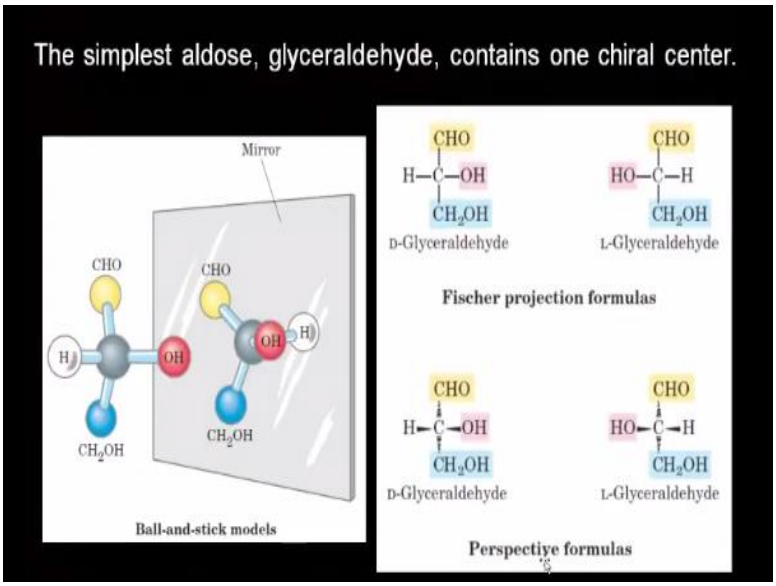

So, in chiral carbon situations you can have two different orientations as we have seen earlier. So, the mirror image, you know this one like here the hydrogen and the hydroxyl group projected towards you and they can have an opposite orientation where the mirror images cannot be superimposed okay. So, two versions therefore are possible and we usually write them in this form.

This is called Fischer projection formula and we know the perspective diagram that we have learned where the bond orientation is shown like the solid wedge shape shows that this

project away from the paper the plane in which it is shown and the dashed wedge means those groups are away from this. Like for example here if you see in the ball and stick model this aldehyde group and this the CH 2 OH they are backwards and these two are front.

And in this you can rotate and have OH on this side as shown here and these two orientations okay HOH like in a more familiar way in the written format I am going to call on the right side or left side okay. It is easy to remember, when it is on the left you say L which is just for memory I am saying. These are just conventions, this does not mean dextrorotatory or levorotatory okay, do not confuse this with the optical rotation although these are optically active.

So, when we have this arrangement like in the way we write when the OH is on the right side it is D glyceraldehyde, when it is on the left side it is L glyceraldehyde okay. So, you can have one chiral carbon, you can have two versions. So the number of stereoisomers possible is 2 power n okay. So, if you have 2 chiral carbons then 2 power 2. If you have 3 then it is 2 power 3 and so on okay.

So, if we go back and look at it this has only one, dihydroxy acetone no chiral carbon. If you take glucose you have 1, 2, 3, 4. So as a result it has 16 different versions possible and of which the 16 can be separated into two groups, eight to the D version like HOH in this orientation and L where this will be on the OHH orientation. So, there are 8 names, D so glucose and so on like D-glucose, D-galactose, D-mannose, D-idose and so on; 8 names and then the same 8 with L.

So, since it is an introductory course, I am not going to introduce all those names or expect you to remember all of them, but at least you should be able to draw the structure of D glucose correctly okay. And this D, L reference we use the carbon that is farthest from this aldehyde group okay. The orientation of the hydrogen and hydroxyl at the chiral carbon that is farthest from the functional group, this aldehyde group.

In this case this will be the one, fifth carbon; 1, 2, 3, 4, 5, 6 this is the fifth carbon. So in this case it is this itself, this is the chiral carbon farthest from this because there is only one and so on okay. So, this is the five membered aldo sugar aldohexose, sorry aldopentose, then you have ribose without the hydroxyl group deoxyribose, this is in RNA, this is in DNA okay.

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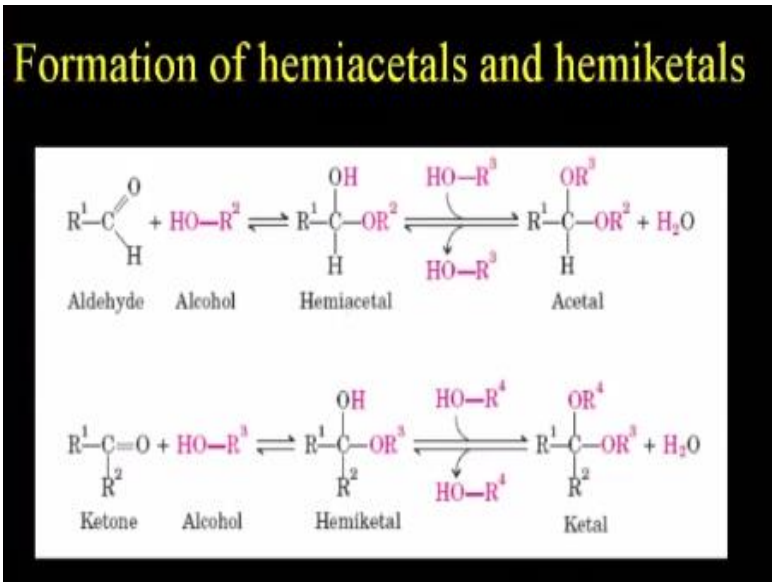

So, the next important feature of carbohydrates is their ability to form intramolecular ring structures okay that comes from this reaction. So, the aldehyde group can react with an alcohol group leading to the formation of what we call hemiacetal okay. So, this carbonyl group gets reduced to hydroxyl group. And since you have another hydroxyl group that can react with another alcohol group like this, then when both are substituted in that manner you call that as an acetal.

So, usually the aldehyde group with one of these hydroxyl groups will form a hemiacetal okay and when that forms you have an additional OH group available and when that OH group, this one, so this is an intramolecular linkage in a typical aldose like glucose and the resulting hydroxyl group when it forms a glycosidic bond with another sugar. So, when the OH group it reacts is intermolecular, it is from another sugar molecule then it forms an acetone okay.

So, glucose-glucose is linked in starch is therefore is an acetyl linkage okay. Similarly, ketone with an alcohol can form a hemiketal and ketal when it reacts with alcohol group of another molecule okay or hydroxyl group from another sugar it forms ketal. So, this reaction is very critical because this is the basis for the ring structure formation.

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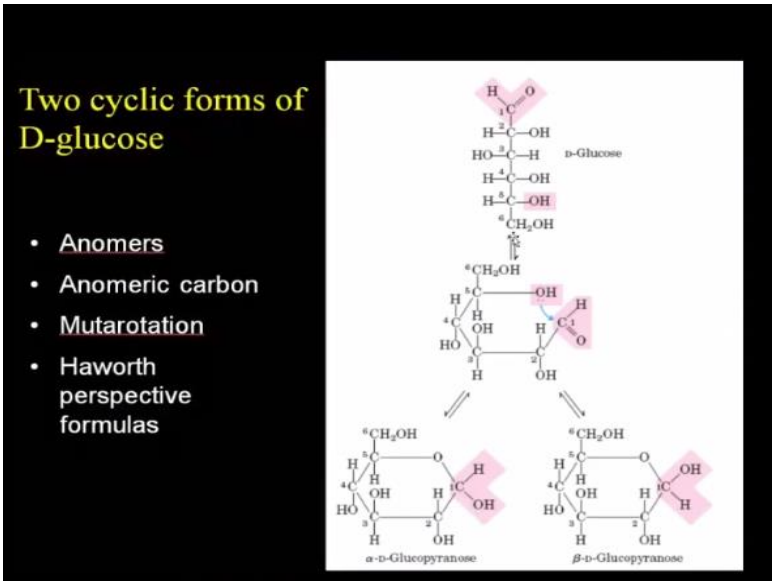

So here you have for glucose this aldehyde group, most often it is with this fifth carbon's hydroxyl group and this reaction aldehyde alcohol condensation leads to a ring structure and this ring structure we usually display in this hexagonal form which is called the Haworth perspective formula. So, this is the Fischer projection formula and this is the Haworth perspective formula.

This is not exactly Haworth, in the perspective formula we would have used those wedge shaped bonding to show the projection as well. But this hexagonal ring is usually referred to as Haworth because Haworth proposed this first. So, an important point to consider here is when this ring structure forms you are generating another chiral center. See this double bond over this carbon is not a chiral carbon.

But once this ring forms it is a chiral carbon and this carbon is called the anomeric carbon okay. And two sugar molecules for example in this case these two differ only in the orientation of the substituents of this carbon, all other groups, the orientation of those groups on these carbons are all same, only here it differs and the sugar molecules that differ in this fashion are called anomers and this carbon itself is called the anomeric carbon.

So, in an aqueous solution, this one orientation we call alpha and the other orientation we call beta, by convention when you show the OH on the top you call the beta and below it is called alpha. So, in starch what you have is an alpha D-glucopyranose okay. So, orientation on this carbon is the reason for D and the orientation around this anomeric carbon is the reason for this alpha. So, the normal glucose is alpha D- glucose okay.

This pyrone will come in a minute while we use this word pyrone as well. So, the main point is this intramolecular hemiacetal formation results in the generation of additional chiral center and that chiral carbon is the anomeric carbon and when two molecules differ in the orientation of the substituents only in the anomeric carbon, they are the anomers. And in solution one form rotates to the other form readily and they interconvert readily and that process we call mutarotation.

These do rotate the plain polarized light. So, the dextro and levorotatory comes from this carbon. And in solution they exist in a certain equilibrium, I think this is more than this, you need not worry about that detail, but the conversion of one optically active form to the other optically active form with respect to anomeric carbon is what is mutarotation okay.

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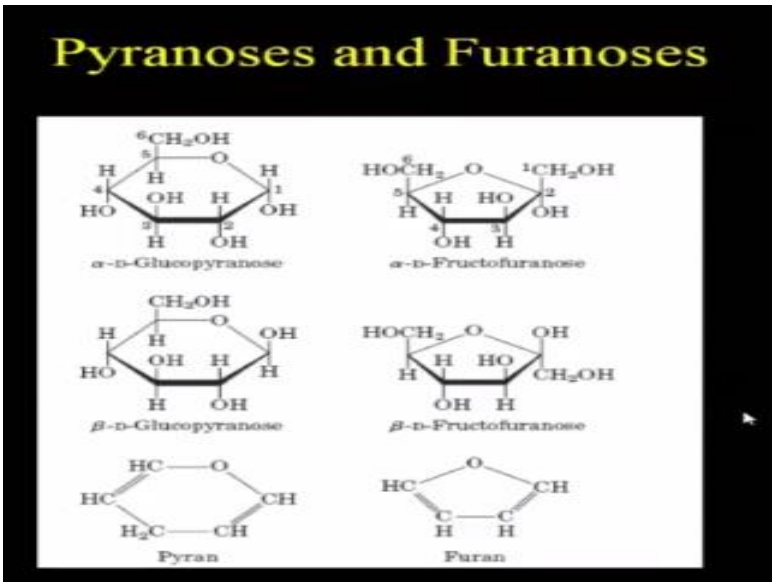

And in this fashion this ring structure resembles the organic molecule pyran and therefore we call them as pyranose. So, the proper chemical name for glucose is alpha D-Glucopyranose. So now you know why is it alpha, why is it D, and why it is pyran. And similarly, these keto sugars they resemble furan and therefore they are furanose. So alpha D-fructofuranose, D comes from the fifth carbon and alpha is from the first carbon that formed the hemiketal structure here. So, this is the basis for the nomenclature of the monosaccharides.

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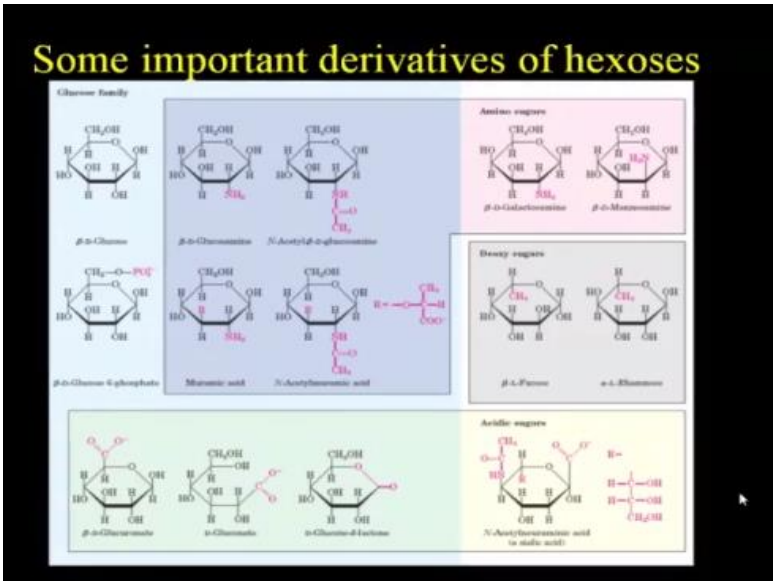

So now we look at some of the derivatives of the monosaccharides that are really important. So, this is the first one, glucose we know very well. So, this is the most common one. So here it is shown in the beta form OH on the top okay. So, the naturally occurring sugars are mostly D version. So therefore, we are going to for our convenience ignore the L versions. So, all of them are going to be D. So, it is D glucose. So here this diagram is beta glucose.

So quite often the second hydroxyl group is substituted with an amino group, so they are called glucosamines and these amines are often substituted with an acetyl group. So, because it is an amino group that is substituted with acetyl group we call this N-acetyl glucosamine. So, these are usually present attached to lipids or proteins in our system as glycoproteins or glycolipids and they become important functionally in many different situations.

So, we will consider them when we get to those actual contexts. S,o these are very prevalent. And in addition you may have phosphate groups. These phosphorylated versions are very important because the phosphorylated versions do not readily get out of the cell. So it helps in trapping the monosaccharides in the cytoplasm because there are no transporters for this phosphorylated versions.

And second this is an activated bond here, compared to this hydroxyl group the alcohol group, this phosphorylated version is more reactive. So, this is an energetic form which is a good substrate for further reactions okay. For example, formation of polymer like glycogen in the liver. So, you have phosphorylated version. Then in addition to this amino group as well as this acetylated amino group.

Sometimes you have an R group in the adjacent carbon the third carbon and that R group is usually lactic acid okay. And this lactic acid substituted and then this lactic acid substituted version of glucosamine, so this structure is glucosamine with the lactic acid we call that as muramic acid. So, this muramic acid also might have acetyl group, N-acetyl muramic acid. So, this is a very important component of bacterial cell wall, we will very soon see that.

And these are some of the modified versions, but basically the major modification is the amino group which gets derivatized with acetyl group and sometimes you might have a lactic acid attached as well. And so this is our other galactosamine, mannosamine like that and some of the sugars might have a methyl group instead of a hydroxyl group in the fifth position; fucose, rhamnose are examples.

They are from mannose and galactose respectively. Then you may have a situation where the aldehyde group, here this anomeric carbon may be oxidized to a carboxylic acid form and they are called as aldonic acids. So, glucose is like gluconic acid that gluconate in the ionized form and they usually react with this alcohol group and form ring structure called gluconolactones.

Some of them may have similar oxidized form in the CH 2 OH sixth carbon and they are called uronic acid, in this case it is glucuronic acid okay, aldonic acid or alduronic acid. Aldonic acid means the first carbon, alduronic acid means it is the sixth carbon that is converted into carboxyl group. So, in addition to these common derivatives, one other important component that we often encounter in our system where usually found in glycoproteins is this N-acetyl neuraminic acid.

This neuraminic do not confuse with muramic, this is muramic this is neuraminic. This is a hexose derivative while this is a 9 carbon. So, the R group has 3 here and they usually have acidic group as well as an N-acetyl substitution as well. The common name is sialic acid and this is a very important modification of glycoproteins required as address tags, we will consider it towards the end of this chapter. So, these are some of the derivatives of the common hexoses that we are familiar with.

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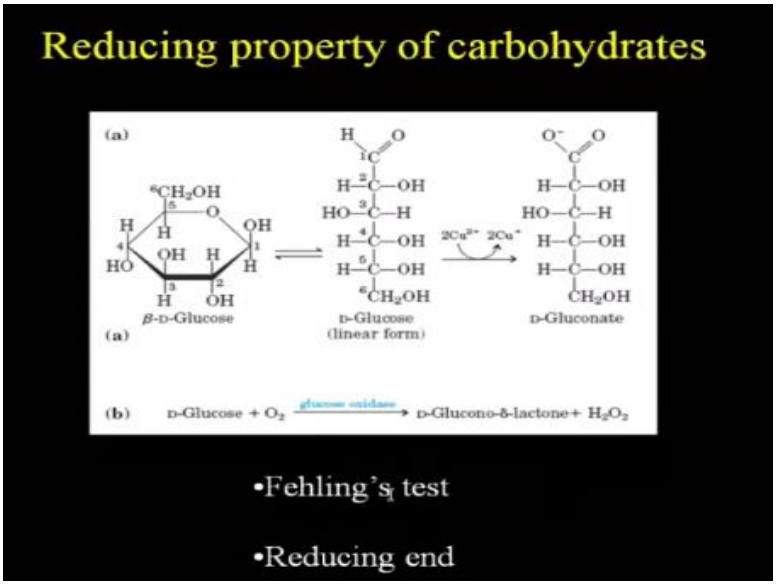

So, a third important property of carbohydrates is their ability to reduce potential oxidants. For example, cupric ion can be converted into cuprous by this aldehyde group. So, this aldehyde group, so this remember this hemiacetal is always in equilibrium with this unlinked form. So, let me go back to it to highlight that point. So this version hemiacetal is in equilibrium with this aldehyde version.

So, if you are going to draw this away through another reaction then it is going to tend towards this to balance and reach equilibrium and therefore more and more of the cyclical form, the intramolecular linkage is cyclical and that will get linearized and used up in the reaction. So, in this version do not ignore its ability to behave like an aldehyde and its ability to behave like an aldehyde is because of this equilibrium.

And so due to this, this one is in equilibrium with this linear form and in the linear form this acts as a reducing agent and such sugars are called reducing sugars okay. So, in a long chain of alpha 1, 4 linkage of glucose like which is the starch or glycogen, so there one end of the chain will have a glucose molecule like this. Its fourth carbon is linked, but the first carbon is anomeric carbon is not linked in glycosidic bond.

So therefore, this can be in equilibrium with aldehyde form and this can reduce. So that end of the amylose chain that has this free anomeric carbon, free in the sense it is not engaged in glycosidic linkage, can act as the reducing end okay so that is the convention for why it is called reducing end. And this ability to reduce is the basis for a test called Fehling's test. So

here the cupric ion becomes cuprous and that in alkaline condition can form a reddish precipitate.

This was the basis for detecting glucose in the blood and used as a diagnosis for diabetes. So you may not have seen anyone doing this, but when I was a kid in school age most of the grandparents when they were diabetic and they were asked to do the glucose measurement in their urine at home itself they will do this test. So, it is standardized readymade thing available and they will do it and they will find it.

The solution itself will be blue. If it is greenish means they are okay, but if it is reddish brown then the sugar level is high. But nowadays we do not do that. We do a lot simpler and more accurate one which is based on this enzyme called the glucose oxidase. So which forms this gluconolactone, remember this structure okay when the aldehyde group is oxidized to carboxyl group.

And when that readily forms this ring this ester linkage carboxylic acid with this alcohol hydroxyl group that is the gluconolactone. And that is what glucose oxidase thus using oxygen as the other substrate you get the gluconolactone. The other product formed in this is hydrogen peroxide which can be converted with the help of another enzyme and that reaction can result in colored product and that is what we measure using peroxidase enzyme.

And remember I have told you about catalase and peroxidase when we were talking about the turnover number. So, using that enzyme we make colored product and since that enzyme has an extremely high turnover number it is extremely sensitive. So very small amount of glucose also can be measured using this two-enzyme coupled reactions. So essentially for measurement the end product has to be colored.

Therefore, you can use a simple calorimeter where absorbance is based on the concentration of the given colored substance and we calculate the amount of glucose present. So, it is all because of this reducing end, this aldehyde group.

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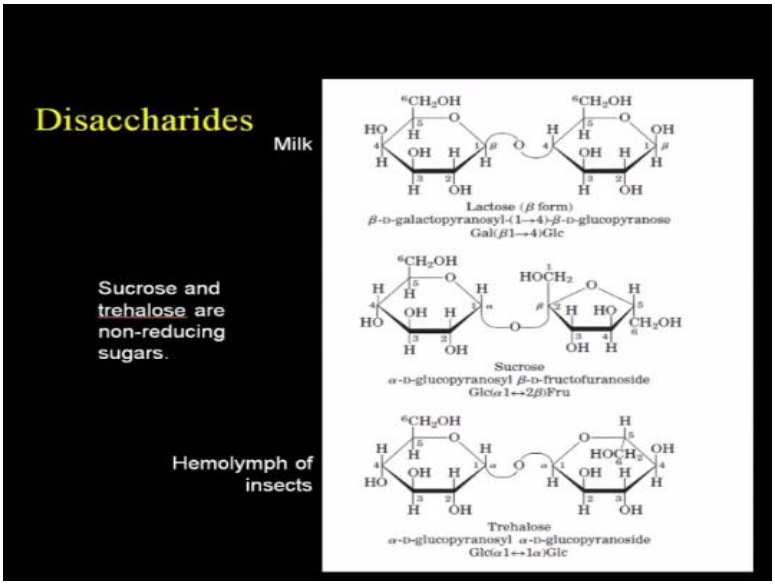

Okay so now we move on from monosaccharides to disaccharides okay. So, again remember the monosaccharides we considered aldoses and hexoses. When I say those two names remember the functional group aldehyde and ketone. Then the other important thing we learnt is hemiacetal, hemiketal formation that resulting in additional center of chirality, so anomeric carbon, these are important concepts.

Then the common derivatives of amino group and the N-acetyl derivative amino group and so on. So the next one we are going to look at the disaccharides. So two glucose molecules in starch itself or cellulose itself is a disaccharide. So, you can consider them as a disaccharide repeating unit. Apart from that there are carbohydrates that exist as disaccharides as such. For example, in milk we have beta D-galactose like this hydroxyl group is shown above the ring and therefore it is beta.

So, beta D-galactopyranose is in glycosidic bond with glucopyranose that is again beta so that beta 1, 4 linkage between galactose and glucose is lactose. This is the primary sugar present in milk, lactose okay. And you have a reducing end here, so therefore lactose is a reducing sugar. And one other important deal I want to tell is when two sugar molecules like for example if you take glucose and another molecule where they differ only in the orientation around one of the chiral centers, they are called epimers okay.

Glucose and galactose are epimers. So, we have learnt enantiomers, diastereoisomers, anomers and epimers. Enantiomers mirror images. Diastereoisomer the same structure but the functional groups are attached to two different carbons such that they are not mirror images,

therefore they are diastereoisomers. If they are mirror images, they are enantiomers. And when the orientation differs only around anomeric carbon, they are anomers.

If the orientation any of the one single chiral center, they are epimers okay. Sucrose on the other hand has an anomeric carbon and another anomeric carbon okay. So here we have inverted the structure, so fifth carbon is here, the first carbon anomeric carbon is here of fructose. So 1, 2 and this is beta orientation and this is alpha orientation this glucose. When you have glucose fructose joined like this this is sucrose.

So here both the anomeric carbons are engaged in the acetal formation, so this is acetal. So this structure is analogous to this okay. So, since we are talking about one of them ketos it is analogous to this structure. So, this itself is if you consider as the internal ring this is like this R is the glucose and this whole thing is the fructose in sucrose. And in such a structure you have no reducing group available and therefore this is non-reducing sugar.

Similar is the case with the Trehalose which is glucose, glucose alpha 1, 1 linkage. This is a disaccharide present in the circulating fluid like the blood equivalent in insects and this is important source of energy for insects. So, these are the common disaccharides that we encounter. So, when you take starch and convert into disaccharide like glucose alpha 1, 4 glucose it is called maltose.

And maltose is often present in some of the cereals and so that is where you have this malt in some nutritional supplements. They are more readily digestible than large starch molecules.

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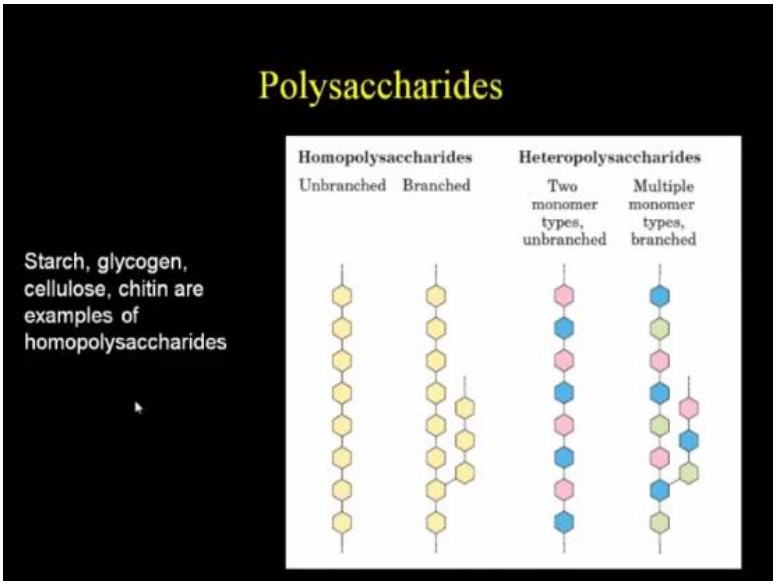

And then finally we move on to polysaccharides. Polysaccharides are quite simple the long chains of monosaccharides. And we already saw alpha 1, 4 in amylose part of starch and we saw the branches alpha 1, 6 branch in amylopectin starch. So, starch therefore as amylose and amylopectin, unbranched and branched versions. And glycogen is more like amylopectin but with a lot more branches than amylopectin.

So, this is the common storage carbohydrate in animals, particularly in liver where it is stored. So, then you may have heteropolysaccharides. These are homopolysaccharides because this all monosaccharides are the same like glucose. So, when you have different monosaccharides are joined they are called heteropolysaccharides. So, you may have two alternating ones and you have multiple ones and so on okay.

So, we will look at structure of some of them like for example one of them we need to look at chitin because we are familiar with starch, glycogen cellulose. Cellulose is glucose but beta 1, 4 linkage. So chitin we will look at.

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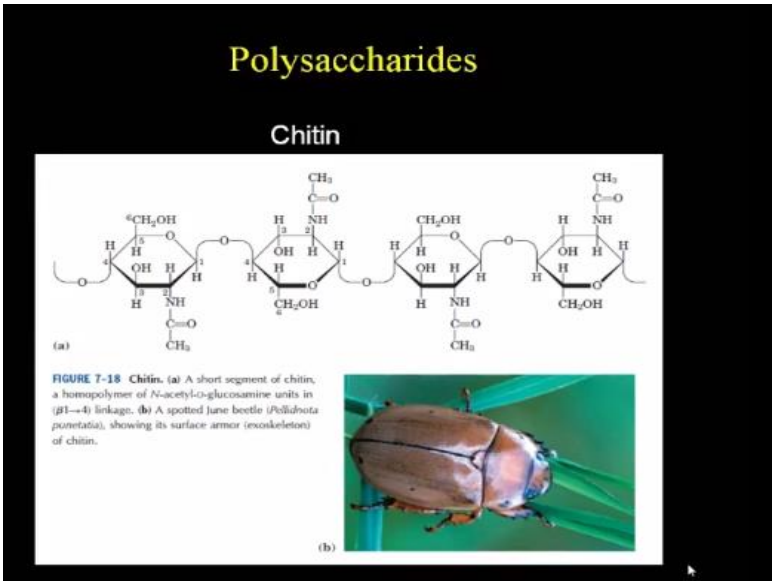

So, chitin is beta 1, 4. So the hydroxyl group is above, so therefore you show like this okay instead of showing it down and this one has an N-acetyl group. So, it is N-acetyl glucosamine. So, this group is N-acetyl glucosamine in beta 1, 4 linkage with N- acetyl glucosamine and therefore it is beta 1, 4. This disaccharide keeps repeating. So, beta N-acetyl glucosamine repeat is what is chitin and that is what is this shiny exoskeleton of insects okay.

So, this chitin, the disaccharide is called chitobiose. And this chitin is the second most abundant organic molecule on earth only behind cellulose. So, you may have seen insects are very large numbers, not only insects, other arthropods like shrimp, prawn, etc. Their exoskeleton also contains chitin. And the chitin molecules are used as biomaterials in tissue engineering as well. So, understanding their chemistry is very useful for many applications too.

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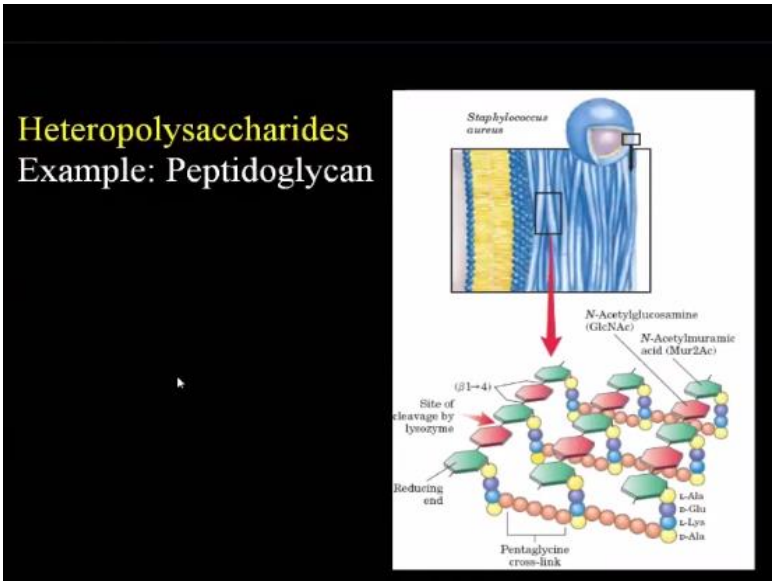

So, the third is heteropolysaccharides. So, what I will do is I will stop here. We will consider heteropolysaccharides and other derivatized form of polysaccharides in the next class. So far, we had minimum derivatization. This N-acetyl amino group is the only addition we have seen. So, we are going to see lot more complex versions and they are very important in our extracellular matrix. So, we will take them up tomorrow.