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A Langmuir film balance study of the interactions of ionic and polar solutes with glycolipid monolayers

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Using a Langmuir film balance experiments have been conducted to discover if dissolved salts or carbohydrates interact with glycolipid monolayers. Two types of glycolipid were studied, simple glycosides made by ether linking monosaccharides to fatty alcohols and cerebrosides extracted from natural sources. It was found that salts or carbohydrates in the subphase expanded glycolipid monolayers. That is, a monolayer spread on a solution occupied a greater area at a given pressure than it would have spread on pure water. Of the carbohydrates galactose and glucose, galactose caused a markedly greater expansion of monolayers than glucose. However, the magnitude of the expansions measured for stearyl glucoside, mannoside and galactoside films on solutions of a particular sugar were not significantly different, demonstrating that this phenomenon is independent of the glycolipid sugar residue. As with carbohydrates, salts also have differing effects on glycolipid monolayers. Although the effect an individual ion has on a monolayer cannot be directly measured, comparisons between salts indicate that there is a correlation between the size of an ion and the extent of the monolayer expansion it causes. To explain these observations two different mechanisms are proposed. In the case of salts it is suggested that large ions which have a low charge density disrupt water structure in such a way that monolayers spread on the surface of their solutions are expanded. The ability of carbohydrates to expand monolayers is explained in terms of the carbohydrate replacing water molecules bound to the polar groups of the monolayer and in so doing increasing the effective area of the lipid molecules. It is suggested that the molecular mechanisms involved in the interactions of ions and carbohydrates with glycolipid monolayers may also operate in the interactions of glycolipids and glycoproteins with extracellular agents and surfaces.

Introduction

The interactions of animal cells with surfaces regulate such fundamental biological processes as growth, differentiation and motility. Although the nature of the interactions is not understood at the molecular level it is thought that the complex glycolipid and glycoprotein molecules which lie at the outer surface of the cells are involved. The oligosaccharide complexes of these molecules are composed of six basic monosaccharide types capable of being combined and disposed in infinite variation and it is an attractive concept that carbohydrate patterns play a major role in cell surface recognition phenomena. In a number of cases this has been found to be so and it is thought that cell surface carbohydrate may regulate immune response; serve as receptor sites for a range of extracellular agents such as bacteria, viruses, glycoprotein hormones and bacterial toxins; be responsible for cell-cell adhesion, via a lectin-type mechanism or via interactions between fibronec-

tins and cell surface carbohydrate; mediate cell differentiation and growth; and its absence be responsible for the loss of contact inhibition of growth in transformed cells [1–3].

In a previous paper [4] we pointed out that the Langmuir film balance could be used to investigate the interaction between carbohydrates and other cell molecules. We envisaged two means of doing this experimentally: (a) establishing the effect carbohydrate dissolved in the subphase has on the pressure-area isotherms of ionic lipids and (b) the effect ionic and polar solutes have on the isotherms of glycolipids. This paper then went on to present the results of experiments of type (a), that is experiments designed to show how various carbohydrates dissolved in the subphase influenced the pressure area isotherms of representative lipids from the various phospholipid classes which make up biomembranes. It was found that monolayers of all the phospholipids were expanded when carbohydrate was dissolved in the subphase, i.e. they occupied a greater area at a given film pressure than they would have if spread on pure water. These experiments suggest a mechanism for the preservative effect carbohydrates have on membranes subjected to osmotic shock, desiccation or freezing.

In the present paper we describe experiments of the second type, that is experiments designed to show the influence materials dissolved in the subphase have on glycolipid monolayers. It is envisaged that glycolipid monolayers spread on solutions of appropriate molecules might provide a suitable model with which to investigate the molecular mechanisms behind the specificity of cell recognition and adhesion which involve cell surface carbohydrate. The glycolipids used are synthetic alkyl glycosides. As far as we are aware no pure naturally occurring glycolipids are commercially available and the synthesis of such lipids is difficult [15]. However, a small number of experiments have been carried out with gluco- and galactocerebroside mixtures to show that the main conclusions drawn from study of synthetic alkyl glycosides are likely also to be applicable to glycolipids of natural origin. The literature on glycolipid monolayers is relatively sparse [6–19].

The experiments reported here are designed to answer the following specific questions: Do carbohydrates dissolved in the subphase expand glycolipid monolayers and, if they do, are the relative capacities of carbohydrates to expand phospholipid and glycolipid monolayers the same? Given that phospholipid monolayers are expanded by carbohydrates in subphase, would glycolipid monolayers be expanded by ions in the subphase? If they are, which ions are most effective and given that galactose has a greater effect on ionic monolayers than glucose [4], will an alkyl galactoside be more expanded by ions in the subphase than alkyl glucoside?

Experimental procedures

Materials

Two types of glycolipid have been used in this study, simple synthetic lipids and cerebroside mixtures. The synthetic lipids, alkyl glycosides, were made by linking monosaccharides to fatty alcohols. The method of synthesis has already been described [4] and is essentially that of Pascher [20]. Four lipids have been synthesized, α-stearyl glucoside, α,β-stearyl galactoside, α,β-stearyl mannoside and α,β-behenyl galactoside. The cerebroside mixtures were purchased from Sigma Chemical Co. Three types are available, a glucocerebroside (from Gaucher's spleen) and two galactocerebrosides (from bovine brain). Each of these has a single polar group, either glucose or galactose, but a mixture of alkyl chains. The type of chains in the glucocerebroside are not specified but in one of the galactocerebrosides they are derived predominantly from nervonic and lignoceric acids and in the other from α-hydroxy fatty acids. We have run each of these cerebroside mixtures on silica gel TLC plates (eluent: chloroform/methanol, 85 : 15, v/v). When the plate is developed all three appear as single spots. The galactocerebroside with α-hydroxy substituted alkyl chains and the glucocerebroside have identical R_F values. The R_F of the other galactocerebroside is slightly greater suggesting that the glucocerebroside has α-hydroxy substituted alkyl chains.

Since the exact structures of these cerebrosides are not known, their molecular weights cannot be calculated and so it is not possible to accurately determine their molecular areas from monolayer measurements. However we have calculated approximate molecular weights by assuming the hy-

drocarbon chains amide linked to the sphingosine moiety are a 50/50 mixture of nervonic and lignoceric acids. For the lipids with α-hydroxy substituted chains 32 was added to this value. Thus the molecular weight values used are 794 and 826, respectively.

Arachidic alcohol (of 99% purity) was also purchased from Sigma.

Five groups of compounds have been dissolved in the subphase so that their interaction with glycolipid monolayers could be measured. They are: (1) carbohydrates, (2) acids, (3) metal ion salts, (4) ammonium and tetraalkyl ammonium ion salts, (5) polyammonium ion salts. In each case the manufacturers premium grade material was purchased. Before lipid was spread on subphases containing these additives the surface was swept with the barrier to determine whether the additive was contaminated with surface active impurities. If it was and a surface pressure could be measured the material was discarded. We could detect no difference between the surface tensions of solutions of these materials and pure water. The carbohydrates, glucose and galactose, were selected because of the marked differences found in the strength of their interactions with ionic monolayers. Two batches of each of the carbohydrates were used. Each batch came from a different supplier. Undoubtedly this is a source of variability in the results. Salts were chosen with which it was hoped that the effects of the individual ions might be separated. For instance all the alkali metal salts are perchlorates. The perchlorate anion, because it is non-nucleophilic, will interact weakly with alkali metal ions. Thus differences in the pressure-area isotherms of glycolipids spread on these salt solutions should be due largely to the differences in the properties of the cations. For similar reasons caesium salts of the halide anions were selected. It was intended that the polyammonium ions serve as protein models and that their interaction with glycolipid monolayers give some indication of the manner in which proteins might interact with the carbohydrate of cell membranes.

The purification of water for the subphase was as described previously [4]. Lipids were spread, depending on solubility, in either 9 to 1 or 4 to 1 hexane-ethanol solutions. The solution concentrations were approx. 1 mg/ml.

Methods

The film balance, its calibration, cleaning, operation and the reproducibility of the measurements made with it have been described before [4]. All the lipids used in this study form stable monolayers, i.e. the surface pressures of their films fall by less than one dyn/cm per minute at film pressure of 30 dyn/cm. All measurements were made at a subphase temperature of 30°C (+ or −0.2°C).

Results

Isotherms of the glycolipids on pure water

Fig. 1 contains the isotherms of the glycolipids on pure water subphases. Curve (d), stearyl galactoside, is representative of all the stearyl glycosides. By comparison a behenyl galactoside film (a) occupies a much lower area at a given surface pressure and has approximately one third the compressibility. Compressibility is taken to be the rate of change of surface pressure with decreasing surface area.

The uncertainty attached to the values of the molecular area calculated for cerebroside films makes comparisons between their isotherms or with those of the glycosides difficult. However some differences are of sufficient magnitude that they cannot simply be the result of errors in estimating molecular weights. Given their chemical

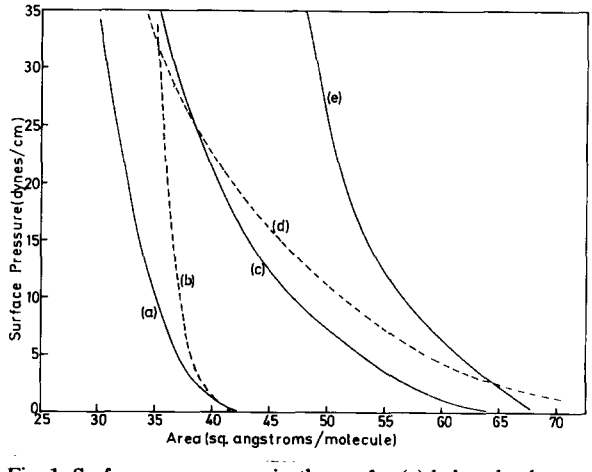

Fig. 1. Surface pressure-area isotherms for (a) behenyl galactoside, (b) α-hydroxy galactocerebroside, (c) galactocerebroside, (d) stearyl galactoside (typical of all stearyl glycosides) and (e) glucocerebrosides.

similarities molecules in the cerebroside films occupy surprisingly different areas. For example, at 5 dyn/cm area values for the gluco and α-hydroxy galactocerebroside films are 61.6 and 38.2 Å^2 per molecule, respectively. Molecules in the α-hydroxy galactocerebroside monolayers appear to occupy less area than molecules in stearyl glycoside monolayers despite the fact that cerebrosides have two hydrocarbon chains and glycosides, one. As might be expected when molecules are tightly packed, α-hydroxy galactocereboside films are practically incompressible. None of the isotherms have discontinuities which would indicate phase changes.

Isotherms of alkyl glycosides on subphases containing glucose and galactose

When either glucose or galactose is added to the subphase the areas occupied by films of all four glycosides are increased in comparison to the areas they occupy on pure water at similar pressures. In Fig. 2 the increase in area is plotted against the concentration of carbohydrate in the subphase. Despite the scatter in the points it is clear that: (1) the increase in film area on a subphase containing galactose is significantly greater than the increase on glucose containing subphases (compare open and closed symbols. (2) There is no significant difference between the area increases measured for each of the stearyl glycosides. (3) Behenyl galactoside is more affected by the presence of carbohydrate in the subphase than the stearyl glycosides.

Since the expansion of glycoside films appeared to be uninfluenced by the nature of the lipid carbohydrate group we measured the effect glucose and galactose have on monolayers of a fatty alcohol. These results are shown in figure three. It can be seen that alcohol monolayers also occupy larger areas on sugar solutions than they do on pure water and that galactose in the subphase causes a greater increase than glucose.

The influence of salts on glycolipid monolayers

Glycolipid monolayers spread on subphases containing salts always occupy greater areas at a given surface pressure than they do when spread on pure water. The area increases for the five glycolipids studied on subphases containing 0.5 M sodium chloride, polyethyleneimine perchlorate

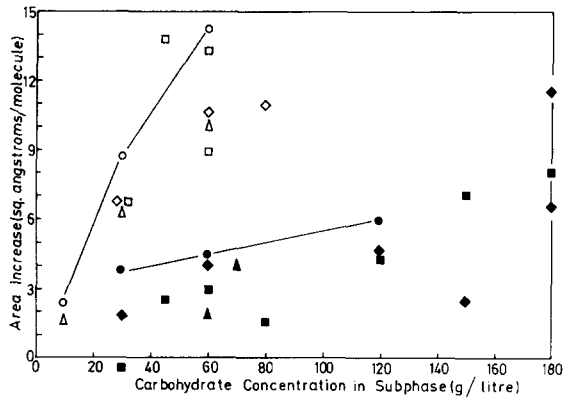

Fig. 2. Plots of the increase in area of glycolipid monolayers versus the concentration of carbohydrate in the subphase. Areas were measured at a surface pressure of 10 dyn/cm. Open symbols denote measurements made on galactose containing subphases, closed symbols on glucose containing subphases. Circles, behenyl galactoside; diamonds, stearyl galactoside; triangles, stearyl mannoside; and squares, stearyl glucoside.

and potassium sulphate are set out in Table I. In general the values obtained are comparable with those calculated for films spread on carbohydrate solutions. However, unlike the carbohydrates where invariably monolayers were expanded more by galactose than glucose, the capacity of ions to expand glycolipid monolayers depends on the nature of the glycolipid. For example compared to stearyl galactoside, stearyl glucoside is more expanded by the presence of potassium sulphate in the subphase but less expanded by sodium chloride. The differences between the cerebroside films spread on potassium sulphate solutions are even more striking. While the increase in area of the galactocerebroside monolayer spread on 0.5 M potassium sulphate is 11.4%, a value similar to those measured for all the cerebroside films on solutions of the other two salts, the area of the α-hydroxy galactocerebroside monolayer is increased by 79.4% and the area of the glucocerebroside monolayer is virtually doubled. These last two percentage increases in area correspond approximately with the maximum values measured for phospholipid films spread on carbohydrate containing subphases. Clearly when glycolipids possess α-hydroxy alkyl chains their packing in membranes may be strongly influenced by the presence of dissolved ions. In all cases but one the

TABLE I

INCREASES IN THE AREAS OF GLYCOLIPID FILMS CAUSED BY IONIC SOLUTES (0.5 M) DISSOLVED IN THE SUBPHASE

All values are averages of two runs. Areas are measured at a surface pressure of 10 dyn/cm and are reproducible to + or −0.2 Å^2 per molecule.

	α-Stearyl glucoside	α,β-Stearyl galactoside	Gluco-cerebroside	Galacto-cerebroside	α-Hydroxy galacto-cerebroside
Sodium chloride	7.69	9.5	5.64	7.81	9.79
Polyethyleneimine perchlorate	1.37	3.87	10.32	3.01	–
Potassium sulphate	10.42	4.88	55.14 [a]	5.32	29.72
Area of film on water	51.03	51.03	56.5	46.75	37.41

[a] 20.84 when the potassium sulphate concentration is 0.42 M.

isotherms of glycolipids on salt solutions are smooth curves with no indication of discontinuities. The exception is the isotherm of α-hydroxy galactocerebroside on 0.5 M potassium sulphate solution which abruptly changes slope at a film pressure of approx. 40 dyn/cm. We observed similar behaviour when certain ionic lipids were compressed on galactose solutions [4].

The areas in Table I were measured at a surface pressure of 10 dyn/cm. Comparing areas at any other surface pressure leads to similar conclusions.

Dissolved salt not only shifts the isotherms of polyhydroxy lipids to greater molecular area but also those of fatty alcohols as the isotherm of arachidyl alcohol run on a sodium chloride solution shows (Fig. 3).

The relationship between the nature of the salt and the expansion of monolayers of behenyl galactoside

In this section an attempt is made to rank ions in order of their capacity to expand glycolipid monolayers. The lipid chosen for these experiments was behenyl galactoside. It is well characterised, unlike the cerebrosides, and as results in previous sections have shown, is the glycoside most influenced by dissolved carbohydrate. We also have to consider the degree of dissociation of the salt. In solution an equilibrium will exist between salt molecules and free ions. In the case of sodium chloride dissociation is essentially complete and we are studying the net interaction of an equal number of sodium cations and chloride anions with the monolayer. On the other hand the salt tetramethylammonium hexafluorophosphate is only sparingly soluble and in its solutions there is probably a significant concentration of ion pairs.

As Fig. 4 shows monolayer expansion is related in a hyperbolic manner to the concentration of the

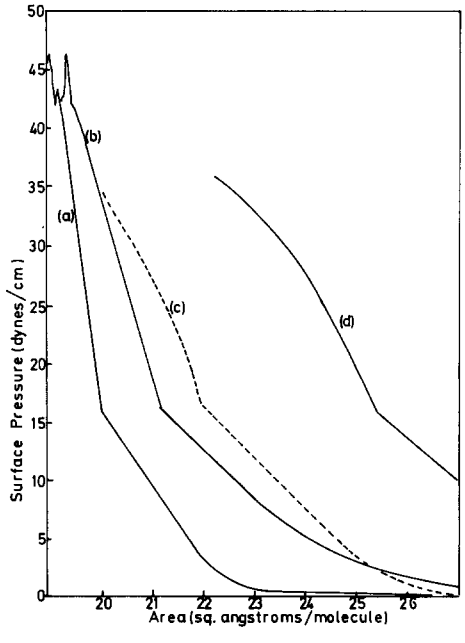

Fig. 3. Arachidyl alcohol isotherms obtained on subphases made up of (a) pure water, (b) 0.17 M glucose, (c) 0.5 M sodium chloride, and (d) 0.17 M galactose.

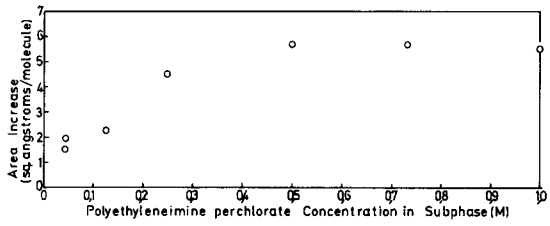

Fig. 4. Plot of the increase in area of a behenyl galactoside monolayer versus the concentration of polyethyleneimine perchlorate in the subphase. Areas were measured at surface pressure of 10 dyn/cm.

subphase additive. In this instance we have measured the expansion of behenyl galactoside on solutions of polyethyleneimine perchlorate. Thus measurements made on two solutions which have different concentrations are not directly comparable. Simply dividing the expansion by the concentration would not provide a concentration independent parameter with which to compare solutes. Because of variations in solubility and the extent to which solutes expand monolayers it is not possible to make all measurements at a single concentration. Thus in Table II the results are divided into concentration groups. To give an approximate idea of how the groups relate to each other a compound sometimes appears in more than one group.

Although for the reasons outlined above it is not possible to make direct quantitative comparisons across the whole range of salts studied, certain trends are clear. Ammonium salts are the most effective at expanding behenyl galactoside monolayers. Of the ammonium ions studied the most effective was the polyamine, spermidine. Te-

TABLE II

INCREASES IN THE AREAS OF BEHENYL GALACTOSIDE MONOLAYERS CAUSED BY IONIC SOLUTES DISSOLVED IN THE SUBPHASE

Areas are measured at 10 dyn/cm. The area of a behenyl galactoside monolayer on water at this surface pressure is 35.08 Å^2 per molecule.

Additive	Monolayer expansion (Å^2/mol)	Additive	Monolayer expansion (Å^2/mol)	Additive	Monolayer expansion (Å^2/mol)
Concn.: 0.01 M		Concn.: 0.09 M		Concn.: 0.25 M	
Tetramethylammonium hexafluorophosphate	2.35	Caesium iodide	13.22	Tetramethylammonium bromide	23.93
Concn.: 0.02 M		Concn.: 0.12 M		Glucosamine hydrochloride	16.49
Tetraethylammonium hexafluorophosphate	4.91	Caesium bromide	7.66	Galactose	16.34
Concn.: 0.045 M		Caesium chloride	7.37	Potassium perchlorate	11.87
Spermidine perchlorate	15.60	Caesium fluoride	5.86	Ammonium chloride	7.09
Polybrene bromide [a]	13.91	Potassium perchlorate	2.75	Sodium perchlorate	6.38
Tetraethylammonium hexafluorophosphate	8.72	Hydrochloric acid	1.76	Lithium perchlorate	6.38
Ammonium hexafluorophosphate	6.08	Sulphuric acid	1.31	Guanidinium hydrochloride	6.18
Ethylenediamine perchlorate	4.92	Concn.: 0.16 M		Glucose	4.66
Imidazole perchlorate	4.38	Ammonium hexafluorophosphate	14.41	Concn.: 0.5 M	
Glucosamine hydrochloride	4.11	Galactose	8.74	Sodium perchlorate	15.79
Hydrazine perchlorate	3.61	Glucose	3.72	Sodium chloride	9.92
Polyethyleneimine perchlorate	1.70	Concn.: 0.20 M		Lithium perchlorate	9.75
Concn.: 0.07 M		Aluminium perchlorate	8.49	Equimolar sodium chloride and perchloric acid	6.24
Caesium sulphate	8.68	Magnesium perchlorate	8.03	Polyethyleneimine perchlorate	5.72
		Trisodium phosphate	5.56	Perchloric acid	2.44

[a] 1,5-Dimethyldiazaundecamethylene poly-methobromide.

traalkylammonium ions rank next, then simple ammonium ions. It will be noted that an amino sugar, such as glucosamine, interacts strongly with both glycolipid and phospholipid monolayers [4]. The remainder of the salts fall roughly into four categories: halides; multivalent ions such as aluminium, magnesium, sulphate and phosphate; small univalent ions such as sodium or lithium, and finally acids, especially perchloric acid. When both perchloric acid and sodium chloride are added to the subphase the monolayer expansion is the average of the values measured on solutions of the pure compounds. The glucose and galactose results are included for the sake of comparison. To produce similar increases in the area of behenyl galactoside monolayers approximately twenty times more sodium chloride would have to be dissolved in the subphase than tetraethylammonium hexafluorophosphate. The salts which have most effect are those which have both cations and anions of large size and low charge density. These salts are also the ones which tend to be least soluble in water. The increases in area of glycolipid films spread on subphases containing either salts or sugars are roughly comparable to those measured for phospholipid films on carbohydrate-containing subphases [4].

One interesting observation was made when behenyl galactoside was compressed on 0.25 M potassium perchlorate solution. With the barrier fully extended the lipid spread normally on the surface of the salt solution. However, as the monolayer was compressed a very thin layer of potassium perchlorate crystallised at the surface of the subphase.

Discussion

Isotherms of the glycolipids

The relatively high compressibility of the glycoside monolayers suggests that they exist in fully expanded, fluid states. These single hydrocarbon chain lipids occupy considerably larger molecular areas than fatty acids or alcohols [21]. Clearly repulsive interactions between carbohydrate groups must play a part in determining the area of their films. It is likely that the isotherm of behenyl galactoside lies at lower molecular area than the isotherms of the other glycosides because these repulsive forces are overcome to a greater degree by the stronger Van der Waals forces between the longer behenyl chains. The slightly lower compressibility of monolayers of this glycoside is undoubtedly a result of tighter molecular packing.

The high compressibility of gluco- and galactocerebroside films suggest that they also exist in fully expanded fluid states. At high film pressures the area per molecule of the galactocerebroside film approaches the area of two hydrocarbon chains (40 $Å^2$/molecule) so the limiting molecular area of this cerebroside seems to be determined by hydrocarbon chain packing rather than carbohydrate-carbohydrate contacts. Without a more detailed knowledge of the structure of the molecular species in the glucocerebroside mixture it is difficult to offer any firm explanation for the very large limiting area of this lipid. Its hydrocarbon chains may be shorter, branched or contain more unsaturation than the other cerebrosides. The incompressibility of the α-hydroxy galactocerebroside monolayer suggests that it forms a solid phase. In common with the galactocerebroside its area seems to be determined by hydrocarbon chain packing rather than interactions between carbohydrate groups.

Mechanism of expansion of glycolipid monolayers by carbohydrates

It is clear from the results that glycolipid monolayers occupy greater areas when carbohydrates or salts are dissolved in the subphase. In our previous paper [4] we demonstrated that dissolved carbohydrate increased the area of phospholipid films and accounted for this behaviour in terms of carbohydrate co-ordinating to and replacing water molecules in the solvation shell of the ions. It was supposed that lipids solvated by carbohydrate as well as water would occupy greater molecular areas. We think a similar phenomenon is responsible for the increase in area of glycolipid films spread on carbohydrate containing subphases. Like ionic monolayers glycolipid monolayers are more effected by the presence of galactose in the subphase than glucose. In general the increases in area of glycolipid films caused by carbohydrates are less than the values found for phospholipids. For example on a 0.17 M galactose solution the area of dimyristoylphosphatidylethanolamine films were

nearly doubled. A similar galactose concentration increased the area of stearyl glycoside films by only 14%. (Fig. 2) This difference might well be a result of hydrogen bonds between ions (or their aqueous solvation shells) and carbohydrates being stronger than hydrogen bonds between carbohydrates.

Galactose caused greater monolayer expansions than glucose irrespective of the nature of the lipid polar group. Fatty alcohols, alkyl glycosides and phospholipids are all more affected by galactose than glucose. This behaviour suggests that carbohydrates co-ordinate to the aqueous solvation shells surrounding lipid polar groups rather than directly to the polar groups themselves.

Mechanism of expansion of glycolipid monolayers by salts

The fact that carbohydrates can expand ionic monolayers by replacing water around the ions raises the possibility that increases in area of glycolipid monolayers on salt solutions are the result of ions co-ordinating to the carbohydrate groups of the lipid. However if this was so then we would expect that since galactose has been shown to have a markedly greater effect on ionic monolayers than glucose, galactolipids would be more influenced by the presence of ions than glucolipids. As the results in Table I show this is clearly not the case. In addition the areas of fatty alcohol monolayers are greater when they are spread on sodium chloride solutions and the percentage increase in area is similar to that observed for glycolipids on solutions of this salt.

Maggio and Lucy [22] and Cadenhead and Bean [23] have suggested that ionic monolayers might occupy greater areas on carbohydrate solutions than on pure water because dissolved carbohydrates alter the long range order of the subphase. In our previous paper [4] we put forward a different explanation for this phenomenon. However, we think that changes in water structure caused by the presence of ions in the subphase might be a valid explanation for the expansion of glycolipid monolayers. The largest expansions of glycolipid monolayers were measured with large ions which have low charge densities. These ions are known as 'chaotropic' or structure breaking and may well produce a change in the long range order of the subphase. That such a change would cause a monolayer expansion is suggested by the work of Ehrstrom et al. [24]. These authors have studied the effects salts have on the fluidity of *Bacillus subtilis* membranes. They found that monovalent salts increased the fluidity of the membrane, fluidity increasing with increasing salt concentration and that at equivalent concentrations 'chaotropic salts' such as potassium iodide had a greater effect than salts like lithium chloride which do not disrupt water structure. An increase in the fluidity of these membranes would be accompanied by an increase in the mean spacing between the lipid molecules.

Such an explanation would be in accord with the very marked effect potassium sulphate has on monolayers of cerebrosides which have α-hydroxy substituted alkyl chains, since a disordering of water structure would be transmitted directly to the packing of the alkyl chains. This would be functionally equivalent to the introduction of branch points or double bonds into the alkyl chain.

Implications for the mechanism of cell surface interactions

The results reported here and in our previous paper suggest that at the molecular level interactions between biomembranes are likely to be complex in nature. We have suggested that the ability of certain sugars, principally galactose and its derivatives, to strongly expand ionic and glycolipid monolayers is the result of the sugar binding to the monolayer and displacing water. It is possible that in certain cases similar interactions are involved in cellular recognition phenomena. Strongly and weakly binding carbohydrates could be disposed in oligosaccharide on the cell surfaces to register with complementary arrangements of ions or carbohydrate residues on extracellular surfaces in a 'lock and key' arrangement.

Localised changes in the fluidity or permeability of the cell membrane may contribute to the initiation of such events as division and differentiation. It is clear that the presence of certain carbohydrates or ions near the polar groups of lipid bilayers alters the spacing of the lipid molecules and therefore membrane properties that depend on lipid packing. Membrane fluidity and permeability are two of these properties.

Acknowledgements

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