Structure and Function of Glycoproteins in Human Saliva

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Contents

Ⅰ. Introduction

Saliva is composed of mixture of various organic and inorganic matter that modulate the oral enironment. Saliva plays an indispensable role for maintenace of healthy conditions in oral cavity. The mucous membranes of oral cavity are lubricated and protected by various salivary mucoproteins and salivary antimicrobial proteins. The other functions of saliva include to keep the oral cavity moist, softening the foods[1]. Xerostomia or dry mouth can lead to accumulation of bacterial debris and to rough mucosal surfaces which bleed easily and are susceptible to infection[2,3]. Over the last three decades, it has been shown that these protective effects of saliva can be attirbuted to particular salivary glycoproteins, such as mucins, fibronctins, proline-rich proteins, histidine-rich proteins, α-amylase and sIgA etc[4]. The structure of these molecules, relationship between the structure and proposed function, and concentrations of these molecules in saliva are being elucidated. Current views on structure and functions of the these salivary glycoproteins, particulary those of mucins, fibronectins, fucose rich protein and sIgA are summarized in this article.

Ⅱ. Structure of Salivary Proteins

A. Salivary Mucoproteins

Human salivary mucoproteins are glycoproteins that have similar biochemical and biophysical properties but also possess distinct structural and functional differences. It has been shown that two mucins exist within submandibular-sublingual saliva namely, MG1,

a high Mr mucoprotein 1, and MG2, a lower Mr mucoprotein 2[5].

MG1, a multiple disulfide-linked subunits protein, has a size of more than 1000 kDa[6-9]. The protein core of MG1 is responsible for less than 15 % of the total weight with the rest being carbohydrate. Amino acid analysis indicates that 43 % of the total amino acid residues are composed of threonine, serine, proline and alanine. Fatty acids are also covalently linked to this salivary mucoprotein. Carbohydrate analysis of the oligosaccharides units released from MG1 by mild alkaline borohydride treatment reveals that MG1 has O-glycosidic bonds between N-acetylgalactosamine and/or threonine and serine. The major oligosaccharides of MG1 range in size from 4 to 16 sugar resides. These represent 78 % of the total weight of MG1, with sulfate contributing an additional 7 %. A putative structure of oligosacchride unit of MG1 is illustrated in Figure 1.

Fluroescence Spectroscopy studies utilizing fluorescent hydrophobic probes, ANS (1-anilino-naphalenesulfonate) and NPNA (N-phenyl-1-naphthylamine) indicates that MG1 binds these molecules, suggesting the exi stence of hydrophobic regions in MG1. Also, The observation that MG1, upon reduction with dithiothreitol, bind to these probes with high affinity, suggests that reduction of disulfide bonds exposes additional hydrophobic domains. However, when treated with Pronase, MG1 showed decreased binding to these probes, suggesting destruction of hydrophobic domains in the protein[10]. In addtion, preliminarry circular dichroism data have indicated that the carbohydrate units of MG1 may have a biased configuration about the core peptide.

MG2, The other human salivary mucoprotein has a size of 200 to 250 KDa. It is composed of a single polypeptide chain which accounts for about 30 % of the total chemical composition[10,11] with the rest mainly being carbohydrates. Amino acid anlysis indicates that proline, threonie, serine, and alanine are responsible for 75 % of the total amino acid residues. A recent study on cloning and DNA sequencing of human MG2 gene reveals that a translated region of 1131 nucleotide encoding a protein of 377 amino acid residues with a molecular mass of 39 kDa. The carbohydrate units of MG2 are ca. 68% of the total weight of and 2 to 7 residues in lenth. They are attached mainly through O-glycosidic linkages to the peptide core. The structures of the major neutral and acidic oligosaccharides from MG2 have been determined and are also presented in Fig 1. The finding that it has ca. 170 carbohydrate units, coupled with the high content of proline, suggests that MG2 may have a "bottle-brush" conformation. MG2 does not bind fluorescent hydrophobic probes such as ANS or NPNA, indicating the absence of hydrophobic regions. Circular dichroism spectrum of MG2 has further suggested that this mucin does not have any ordered secondary structrure, displaying random coil. Physicochemical characteristics of these salivary mucins are summarized in Table I. A recent report[12] suggest that besides MG1 and MG2, there might be two other high Mr mucin species, one with buoyant densities of 1.56 g/ml and the other one with buoyant density of 1.48 g/ml. Details of physicochemical characteristics of them are not known.

B. Fucose-Rich Glycoprotein (FRG)

Fucose-rich glycoprotins (FRG), a calcium-dependent salivary agglutinin binds and can agglutinate serotype c strains of *Streptococcus*

mutans in the presence of calcium ion; 0.1 μg of the agglutinin can cause a rapid aggregation of ca. 10^8 bacteria[13,14]. FRG has been prepared from human parotid saliva by affinity adsorption of the presumptive salivary agglutinin to the microorganisms, and followed by desorption with a 10 mM phosphate buffer. The protein was purified to apparent homogenity by employing preparative ultracentrifugation, ultrafiltration and gel filtration chromatographic procedures. Subsequent analysis of the isolated protein revealed that the multisubunit glycoprotein has a size of at least 5 x 10^6 determined by gel filtration chromatography and PAGE with a subunit size of ca. 440 kDa determined by SDS-PAGE. Amino acid analysis indicates that it has a high content of aspartic acid, serine, and threonine while proline content is low. The protein contains 45 % carbohydrate and is rich in fucose, but the nature of the linkages to the protein region has not been elucidated. The biochemical properties of FRG are summarized in Table I.

C. Secreotory IgA (sIgA)

IgA is the predominant immunoglobulin in external secretions, including saliva, in contrast to serum. As the IgA system is described in detail in the number of textbooks and review articles, only its structural and functional characteristics will be briefly described here. Salivary sIgA is produced by cells of B

Table I: Biochemical Characteristics of Salivary Glycoproteins*

Properties	MG1[a]	MG2[b]	Amy[c]	FN[d]	FRG	sIgA
Size (kDa)	>1000[e]	200-250	55-60	220-240	440	385
Subunits	Yes	No	No	2	>10	Yes[h]
Protein content	14.9 %	30.4 %	93-94%	88-95 %	55%	83-93 %
Carbohydrate content	78.1 %	69.0 %	6-7 %	5-12 %	45%	7 -11 %
Sulfate content	7 %	1.6 %	0 %	< 0.1 %	?	0
Size of oligosaccharides	4-16 residues	2-7 residues	11-12 residues	9-13 residues	?	1 -12
No. of oligosaccharides	292	170	4	3-6	?	4 - 9
Glycopeptide linkage	GalNAc-Thr/Ser	GalNAc-Thr/Ser& GlcNAc-Asn	GlcNAc-Asn	GalN-Ser/Thr &GlcN-Asn	?	GalN-Ser/Thr GlcN-Asn
Covalently bound fatty acids	5-10	Negligible	0	0	0	0
Quantity[f]	?	14-203 μg ml (HSMSL)[i]	650-800 μg/ml (HSP)[j]	0.2-2 μg/ml (HWS/HSMSL) 2-6 μg/ml (HPS)	?	96-102 μg/ml

a. High molecular weight salivary mucin. b. Low molecular weight salivary mucin.
c. α-Amylase. d. Fibronectin e. fucose rich protein f. secretory immunoglobulin A
g. Estimated by its elution position at gel filtration chromatograaaphy.
h. primarily as dimer: J chain and secretory component are also covalently linked to IgA molecule through disulfide bond.
i. HSMSL: human submandibular-sublingual saliva j. HPS: Human parotid saliva

*: Adapted from "Salivary glycoprotein" by Robert E. Cohen and Maichael J. Levine in Human Saliva: "Clinical Chemistry and Microbiology Vol I (ed. by Jorma. O. Tenovuo" CRC Press Inc, Boca Ration, Florida, 1989

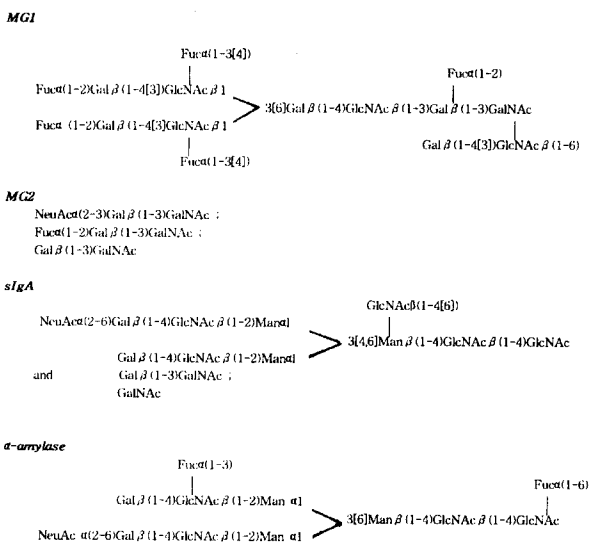

Fig. 1. Carbohydrate structure of salivary glycoproteins

lymphocyte lineage within the major and minor human salivary glands.

Immunofluorescence studies have localized IgA-containing plasma cells mainly in the connective tissue around intercalated or intralobular ducts. J chain is usually found within IgA-secreting plasma cells as welll. Secretory component has been localized within epithelial cells of the intercalated and intralocular ducts [15 17]. IgA consists of two identical heavy chains and two idential light connected by disulfide bonds. The class and subclass of immunoglobulins are determined by their distinct heavy chain type where, in the case of IgA, an additional C-terminal extension onto the heavy chain permits monomer cross-linking and IgA dimer formation via interchain disulfide bonds. The N-terminal region of this molecule contains the two antibody combining sites. Within serum, IgA exists primarily as monomers, while within secretions, secretory IgA (sIgA) is composed of a 385 kDa complex consisting of a 300 kDa IgA dimer, a 70 kDa secretory component, and a 15 kDa J chain. Except the light chains, all of the chains contain N-linked oligosaccharide units, as described in Table I and Figure 1.

Two subclasses of IgA heavy chains are known to exist, IgA1 and IgA2. The major differences between these subclasses comes from their difference in their amino acid sequence in the hinge region. IgA1 includes a duplicated eight amino acids, proline-rich sequence, which also contains five O-linked oligosacharides[18,19]. The disulfide linkage between the light and heavy chain also occurs in this region. In contrast, IgA2 contains a short sequnce of consecutive proline residues in the hinge region and does not contain O-linked oligosaccharide unit. The covalent structure of the polypeptide and carbohydrate moieties of the sIgA molecules has been determined[18,20,21]. The free SC (secretory components) is a monomeric glycoprotein, consisting of 558 amino acids, with 7 N-glycosidically linked carbohydrate chains representing 23.4 % of the total wieght of this species. The protein has no methionine but has 20 cysteine residues that form 10 S-S bridges. The polypeptide chain also appears to be divided into 5 regions of internal homology, of 104 to 114 amino acids in length. J-chain is also a glycoprotein containing a single N- linked oligosaccharide. The carbohydrate content of IgA is variable and depends on the heavy chain subclass; both O- and N- glycosidically linked oligosaccharides units may be present, representing 7 to 11 % of the total weight of the IgA molecule. Carbohydrate stucture of IgA is illustrated in Fig. 1.

D. Fibronectin (FN)

Fibronectins are high molecular weight ad-

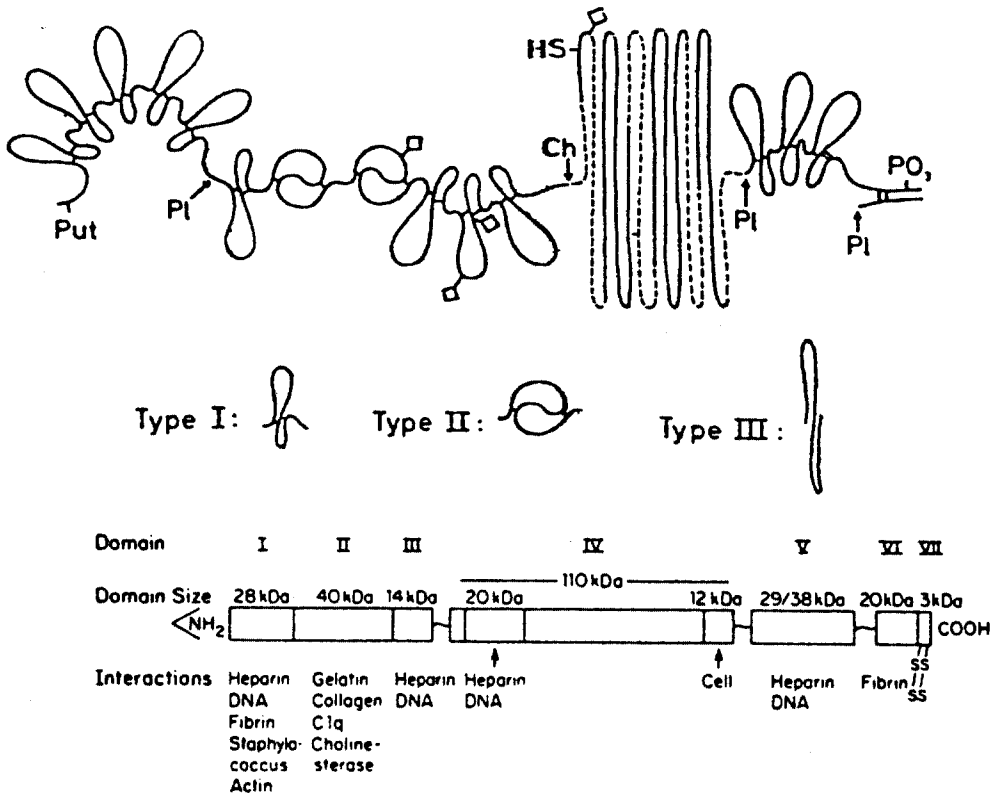

Fig. 2. Domain Structure of fibronectins.

hesive glycoproteins that occur at cell surface, extracellular matrix, connective tissues, and body fluids including blood[22-24]. Immunocytochemical techniques have been used to localize fibronectin within ductal cells of human minor salivary glands. Fibronectin has been also detectd in the gingival crevicular fluid, in human whole saliva, and in salivary gland secretions[25-26]. In general, human fibronectins have a Mr of 440-480 kDa with a subunit size of 220-240 kDa and contain 5 to 12 % carbohydrate. The salient features of fibronectin are summarized in Table I. Human plasma fibronectin occurs as a disulfide-linked dimer joined near the C-terminus of both chains, with one subunit chain being slightly larger than the other. Cellular fibronectin is structurally similar but not identical to plasma fibronectin. Primary sequence information obtained from cDNA clones revealed that different subunits which differ in parts of their primary sequence, all arise form a single large gene composed of multiple small exons that are identical over much of their sequence. Fibronectin consists of a series of homologous repeats, containing disulfie-bonded loops of 45 to 50 and 90 amino acids long, which make up about 90 % of the entire sequence of this molecule. Domain structure of fibronectins is illustrated in Fig. 2. Biophysical studies indicate that fibronectins are composed of highly structured globular domains separated by flexible at extreme salt concentrations of pH. Fibronectin undergoes a substantial amount of

posttranslational modification. Transglutaminase reactive sites have been localized near the amino terminus of the protein. The positions of some of the oligosaccharide side chains have been located within the collagen binding domains. Evidence also exists for the variable phosphorylation of serine residues throughout the fibronectin molecules (27). However, the functional significance of these various post-translational modifications remains obscure.

III. Functions of salivary glycoproteins

A. Buffering Action

Bicarbonate ion and to an less extent histidine-rich protein and phsophates contribute to maintain pH in oral cavity, and in the esophagus. The salivary mucins that have large Mr also contribute to maintain local pH gradient by acting as diffusion and permeability barriers as is the case of intestinal mucins[29,30].

B. Digestion

Role of saliva in the digestive process in conjunction with various protective functions, is relatively minimal. Saliva facilitates formation of the food bolus to allow for efficient mastication and swallowing[31]. In this regard, the salivary amylase and, to a lesser extent, lipases most likely contribute to the initial stage of digestion. Salivary amylases function in the initial steps of food breakdown by initiating the breakdown of susceptible foods via hydrolysis of α(1->4) glycosidic linkages in carbohydrates[32,33]. Due to the comparatively short time that food actually remains within the oral cavity, it is likely that the digestive role of salivary amylase is minor at best. In addition, salivary glycoproteins (e.g. mucins) may also assist in preparation of the food bolus by imparting their lubricatory and viscocity properties to the food.

C. Lubrication

During mastication, saliva provides protection by lubricating and mechanically cleansing the oral tissues and flushing away debris. The role of salivary glycoproteins in lubrication has recently been demonstrated[31]. Lubrication is a property of oral pellicles which may protect surfaces against mechanical disruption or abrasion. These properties apperar to be dependent on the presence of glycoproteins capable of forming boundary interfaces at tissue surfaces moving relative to each other and not directly related to the viscocity of the fluid. It has been reported that relative lubricating ability of the salivary glycoproteins was found to be MG1 > MG2 > PRG. Other salivary glycoproteins, including lactoferrin, amylase, and secretory IgA also possessed lubricating abilities which were found to be significantly higher than either human serum albumin or a simulated salivary buffer control. The lubricating properties of a number of salivary glycoproteins may be derived, to a significant extent, from the carbohydrate domains of these molecules. Deglycosylation of the PRG resulted in a marked decrease in the lubricating ability relative to the intact molecule[32,33].

D. Interaction with other salivary proteins.

Several salivary glycoproteins are known to bind noncovalently with other salivary proteins. One of the functions of these noncovalent interaction is for one molecule to act as a

"carrier" to bring other macromolecules to the destined site in oral cavity. The protein complexes could act as functional units by playing different role from those of the each components. Salivary mucins interact with lysozyme, sIgA and lipids[34,35]. In this case, the salivary mucoproteins may behave as " carrier molecules", that bind to and concentrate protective molecules at various site in oral cavity. It has been recently reported that fibronectins bind a salivary glycoprotein with characteristics similar to amylase[36]. Adherence of type I fimbriated strain of *E. Coli* to epithelial tissues could be inhibited by this interaction.

E. Antimicrobial Activity

Salivary glycoproteins have antibacterial and antimycotic activities. The salivary peroxidase system elict a direct toxic effect on various microorganisms, including *S. mutans*, *S. fecalis* etc. by caltalyzing the oxidation of SCN^- ion by H_2O_2 to OSCN . All strains of S. mutans studied are inhibited by the salivary peroxidase system. The secretory immune system of saliva also has a anti-microbial activity suitable for mucosal defense.

In general, secretory immunoglobulins protect tissues by acting as first line defender. Aggregation of microorganisms by sIgA would retard their movement and hinder their invasion into deeper tissues. It has been reported that sIgA from parotid saliva inhibit the adherence of certain strains of *streptococci* to human buccal epithelial cells. It is also suggested that sIgA may inhibit the adherence of these organisms to hard tissue surfaces in the oral cavity[37-40]. sIgA has direct microbiocidal effects on microorganisms. It has been shown that lymphocyte, and neutrophils, and macrophages have receptors specific for IgA and this promote antibody-dependent cell mediated cytotoxicity of IgA-sensitized target cells *in vitro*. Also, sIgA can activate complement by the alternative pathway, which leads to killing on mucosal surfaces[41,42]. Fibronectins (FN) could act as a antimicrobial agent by binding bacteria such as *S. aureus*. It has been shown that FN bind numerous Gram(+) bacteria and that they were capable of mediating the binding of these microorganisms to epithelial cells[43,44] while they appear to act as a barrier against the adhesion of various Gram(-) bacterial strains. Binding of salivary α-amylase to *S. sanguis* and *N. gonorrheae* has been reported[45-46] as has the binding of the FRG with *S. mutans*. It exerts inhibitory effect on *N. gonorrheae* by possiblly acting on the gonococcal outer cell wall[46]. Detailed mechanism and significance of these interactions, however, have not been determined. It has been also demostrated that MG2 interacts with several strain *S. sanguis* and *S. mutans* and that removal of the sialic acid residues of MG2 diminishes interaction with *S. sanguis* but not *S. mutans*. It is interesting to note that saliva might contain inhibitors of HIV-1 replication. When mucin-rich fractions from gel filtration column chromatography was subjected to a plaque assay on HeLa CD^- cell monolayer, it reduced infectious units by 75 %[47]. Little information is available on the antimicrobial activities of the other salivary glycoproteins.

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국문초록

인체 타액내 당단백질의 구조와 기능

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한 송

타액은 구강 환경을 조절하는 여러가지 유기질과 무기질의 혼합물로 구성되어 있다. 구강 점막은 여러 타액 점액 단백질과 타액 항세균 단백질에 의해서 윤활이 되며 보호된다. 타액의 다른 작용은 구강 점막을 축축하게 하고 음식을 부드럽게 한다. 구강건조증은 세균의 침착을 야기시키거나 점막면을 거칠게 하여 출혈이 되기 쉽게 하며 이로 인해 감염이 야기될 수 있다. 이러한 타액의 보호 작용은 mucin, fibronectins, proline-rich glycoproteins, histidine-rich proteins, α-amylase, s-IgA 같은 특별한 타액 당단백질에 기인한다고 하는 것이 지난 30년 동안에 알려져 있다. 이러한 분자들의 구조, 구조와 기능사이의 관계, 타액내 이러한 물질들의 농도에 관한 것들이 알려지고 있는 중이다. 이러한 타액 당단백질 특히 mucin, fibronectin, fucose rich-protein과 s-IgA의 구조와 기능에 대한 현재의 견해들을 이 논문에서 요약하고자 한다.