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Review

A role for carbohydrate recognition in mammalian sperm-egg binding

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ABSTRACT

Mammalian fertilization usually requires three sequential cell–cell interactions: (i) initial binding of sperm to the specialized extracellular matrix coating the egg known as the zona pellucida (ZP); (ii) binding of sperm to the ZP via the inner acrosomal membrane that is exposed following the induction of acrosomal exocytosis; and (iii) adhesion of acrosome-reacted sperm to the plasma membrane of the egg cell, enabling subsequent fusion of these gametes. The focus of this review is on the initial binding of intact sperm to the mammalian ZP. Evidence collected over the past fifty years has confirmed that this interaction relies primarily on the recognition of carbohydrate sequences presented on the ZP by lectin-like egg binding proteins located on the plasma membrane of sperm. There is also evidence that the same carbohydrate sequences that mediate binding also function as ligands for lectins on lymphocytes that can inactivate immune responses, likely protecting the egg and the developing embryo up to the stage of blastocyst hatching. The literature related to initial sperm-ZP binding in the three major mammalian models (human, mouse and pig) is discussed. Historical perspectives and future directions for research related to this aspect of gamete adhesion are also presented.

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Contents

1. Introduction

The very first cell–cell interaction in the life of sexually reproducing metazoans is the binding of sperm to the surface of the egg. The matrix covering the egg is highly specialized to ensure that robust binding occurs, initiating the process of fertilization. Rapid species-specific binding is also obligatory during external fertilization in an aquatic environment, especially in the presence of closely related species within the same ecological niche [1]. There are many barriers that block reproduction between different mammalian species, so the requirements for species-specific binding are more relaxed [2,3]. A notable exception is the restricted specificity of human sperm that bind only to the zona pellucida (ZP) of hominids like the gorilla and gibbon [3,4].

The concept that sperm-egg binding involves carbohydrate recognition was initially proposed by Monroy nearly fifty years ago [5]. This specificity was based on the sensitivity of gamete binding to mild periodate oxidation of the jelly coat encasing eggs in lower

Abbreviations: ZP, zona pellucida; NK, natural killer; SRS, species recognition system; EBP, egg binding protein; SLEX, sialyl-Lewis^x; MS, mass spectrometry; HZA, hemizona assay; Cer, ceramide.

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marine species. Sodium *m*-periodate under carefully controlled conditions selectively oxidizes vicinal hydroxyl groups associated with oligosaccharides and polysaccharides coating the surface of eggs [6]. Sperm-egg binding was the first cell–cell interaction that was clearly shown to depend on carbohydrate recognition based on this specific chemical sensitivity.

Propagation is an absolute imperative for the survival of any species. In higher organisms, a functional immune response that targets pathogens and tumor cells is also essential for individuals to survive long enough to generate fertile progeny. These overlapping imperatives suggest that the immune and reproductive system must be highly integrated to enable such responses against pathogens while simultaneously protecting gametes and the developing fetus in utero from injury. Immune cells usually recognize cells, tissues and organs via their major histocompatibility (MHC) class I antigens [7]. This recognition of self in the immunological context is necessary to prevent aberrant responses against healthy cells and tissues while enabling highly specific targeting of pathogens and tumor cells. However, gametes and many other cell types in the human body completely lack MHC antigens, or express these molecules at a very low level [8]. This lack of MHC expression places these cells at risk for lysis by natural killer (NK) cells based on the missing self hypothesis [9].

A species recognition system (SRS) has previously been hypothesized to prevent the lysis of MHC class I negative cell types [10]. The SRS relies on a system of lectins bearing domains that inhibit immune responses (e.g. immunoreceptor tyrosine-based inhibition motifs or ITIM) or that can form a complex with a protein possessing immune-modulating activities. By working together, the SRS and the MHC system enable immune recognition of all types of cells and tissues in mammals. This SRS is also employed during initial sperm-egg binding during the process of fertilization [10]. For this reason, the SRS likely predates the MHC system for the recognition of self, which developed later to enable more precise targeting of pathogens and tumor cells. The potential linkages between gamete and immune recognition in the context of the SRS have previously been reviewed [11].

The evidence that initial sperm-ZP binding in the human, mouse and pig relies primarily on carbohydrate recognition is now quite substantial. The primary focus of this review is to emphasize the implications of this specificity of binding and discuss future directions.

2. Human sperm-ZP binding

For many years, the mouse was the predominant model for mammalian gamete binding interactions. The assumption was that data

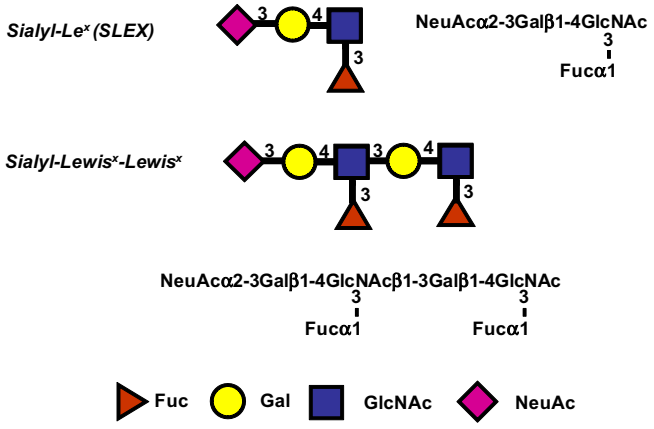

Fig. 1. Major terminal carbohydrate sequences expressed on the surface of the human ZP.

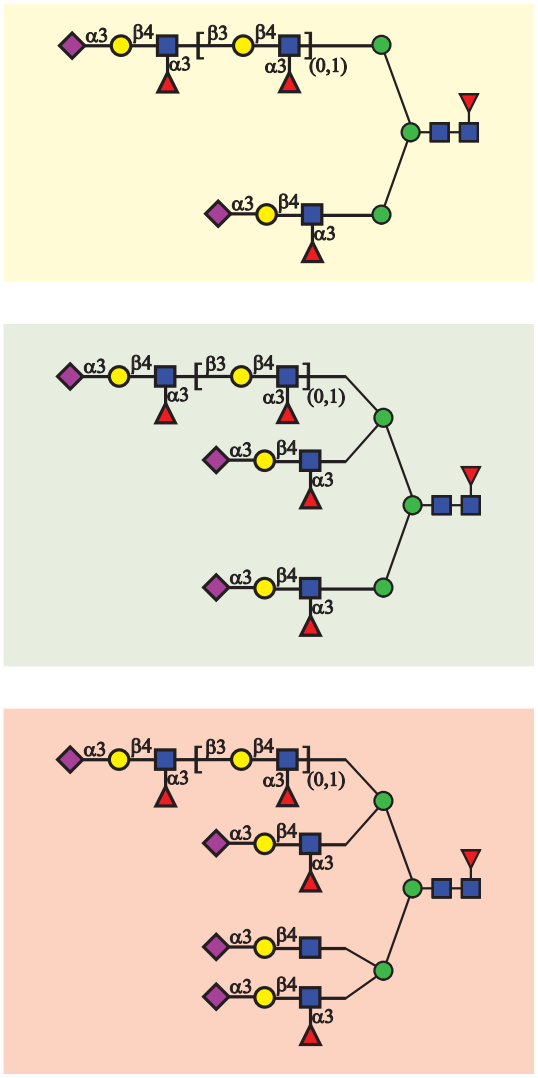

Fig. 2. Major N-linked glycans expressed on the surface of the human ZP. This figure was previously published [14].

obtained in the mouse model could be directly extrapolated to the human model, but recent studies indicate otherwise. The human has now become the predominant model for investigating sperm-ZP binding interactions that have translational value in the clinical setting. A definitive review on the role of carbohydrate recognition in human sperm-ZP binding, including a brief historical perspective, has recently been published [12]. Another review focused on the identification of the egg binding proteins (EBPs) associated with human and mammalian sperm is also available [13].

The most definitive study on human sperm-ZP binding was published in 2011 [14]. The human ZP is profusely coated with carbohydrate sequences known as sialyl-Lewis^x (SLEX) and sialyl-Lewis^x-Lewis^x (Fig. 1). A summary of the major types of the core fucosylated N-glycans associated with human ZP is also shown (Fig. 2). Terminal SLEX is expressed on about 85% of all the N-glycans, usually in multivalent presentations. SLEX tetrasaccharide and SLEX-BSA neoglycoprotein inhibit human sperm-ZP binding in the hemizona assay (HZA) by 70% at final concentrations of 500 μM and 2 μM, respectively [14]. These findings are consistent with a previous study indicating that 79% of human sperm binding in the HZA relies on lectin-like interactions, with protein–protein interactions responsible for the remaining activity [15]. SLEX is also a ligand for all three selectins and Siglec-9, consistent with the SRS paradigm [16–18].

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