



Pig Immunology Cognition as a Prerequisite to Maintaining Pig Health: A Review

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Abstract

The review highlights pig immunology as essential for maintaining good health and welfare in pigs. The innate immune system includes physical barriers and immune cells such as neutrophils and macrophages, while adaptive immunity involves B and T cells, along with dendritic cells. Pigs' cells develop memory immune responses, enabling a quicker and more effective defense when re-exposed to specific pathogens, initiating an antibody and antigen response. Pigs' immune system is a complex mechanism and similar to that of humans, with innate and adaptive responses working synergistically to protect against pathogens. Immune response genes in pigs play important roles in disease resistance. The key genes are: Major Histocompatibility Complex (MHC), for example, Swine Leukocyte Antigen (SLA) in pigs. The Cytokine genes, such as interleukins and interferons, and pattern recognition receptors (Toll-like receptors). These genes are important for disease resistance, vaccine development, and breeding programs, where selection for favourable immune responses can enhance the overall health of pigs. Macrophages and dendritic cells play a major role in linking the innate and adaptive immune responses. They are specialized antigen-presenting cells equipped with a wide range of pathogen-recognition receptors that identify conserved microbial molecular markers, known as pathogen-associated molecular patterns. Knowledge in pig immunology ultimately enhances overall health and productivity. Identifying genes that control immunity in pigs can assist in selecting animals with quicker responses to disease challenges and aid in vaccine development against economically important diseases that affect productivity, increase production costs and constrain livestock management, including antigenic restrictions on species and breed selection.

Introduction

Pigs are valuable domestic animals, and valuable for agriculture and veterinary science research (Javed *et al.*, 2024). The immune system is a complex and specialized system that helps the body respond to and resist microorganism invasions (Pig 333, 2017a). It is a collection of biological structures and processes in an organism that fight disease by recognizing and eliminating pathogens and tumour cells. Immunology is the scientific field that investigates how animals distinguish between their own components and foreign

substances, generate responses against foreign invaders and retain memory of these encounters for future protection (Sanchez-Vizcaino, 2001).

The immune system plays a critical role in protecting animal health and promoting overall well-being (Klasing, 2001). However, vaccinology applies immunology to address infectious diseases which affect animal health, welfare, farm economics, and human populations' exposure to zoonotic risks from established and emerging pathogens (Murtaugh *et al.*, 2014). In recent years, the growing importance of swine in agriculture has led to an increased focus on research dedicated to swine (Saalmiiller, 1998). It is tasked with detecting a diverse range of agents, such as viruses and parasitic worms, while differentiating them

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from the body's healthy cells. Measurement of immune responsiveness can serve as an indirect indicator for disease incidence or animal health status, with immunological traits being linked to performance (Clapperton *et al.*, 2008).

The immune response to pathogens and antigens is effective but complex, as pathogens evolve rapidly to evade detection, adapt to circumvent the immune system, and successfully infect hosts (Thacker, 2003). Therefore, immunology is the study of the immune system and its components. Javed *et al.* (2024) reported that understanding the porcine immune system is crucial for raising healthy pigs without antibiotics, leading to the development of alternative health strategies like specialised diets.

Immunology is important for the maintenance of good health and disease prevention. It is a prerequisite to the development of vaccines, drug precision, disease prevention and treatment, organ grafting, and autoimmune disease management. An optimal immune response is essential to prevent infectious diseases, as both under-responsiveness and over-exuberant responses can lead to health issues (Klasing, 2001). Traditional strategies like vaccination and strict biosecurity measures enhance the overall immunocompetence of healthy animals and are effective ways of preventing and controlling infectious diseases (Bai and Plastow, 2022). Given the inadequate understanding of the pig immune system among pig farmers and industries, for good health (Ballester *et al.*, 2023), the review thus demonstrates pig immunology as a prerequisite for maintaining good pig health and welfare.

Concepts of Immunity- Natural and Adaptive Immunity

There are two concepts of immunity: natural and adaptive immunity. Natural immunity is less precise in identifying foreign antigens and organisms, and its reaction does not improve with repeated exposure. Previously considered a non-specific defence barrier in pigs against infections without prior immunization, recent research has revealed otherwise (Thacker, 2003; Page, 2021). The innate immune response is rapid and is followed by early-induced responses that do not confer long-lasting immunity. It involves phagocytic

cells, natural killer cells (NK), and interferon, and occurs within minutes or hours of the threat. If this initial defence is overcome, adaptive immunity is activated. The host's defence mechanisms typically identify and neutralize most encountered organisms swiftly to prevent infection (Sanchez-Vizcaino *et al.*, 1981 and Sabir and Jan (2025)). Adaptive immunity develops in response to foreign molecules or antigens, triggering a targeted response to an external stimulus. Once antigens are recognized and captured, various mechanisms activate lymphocytes to produce antibodies and cytokines. Immunology has evolved steadily from its origins to the present day, with significant advancements, particularly in porcine immunology, occurring in recent decades (Sanchez-Vizcaino *et al.*, 1981). These developments have helped improve knowledge of the different immune mechanisms in the porcine species: The development of syngeneic pigs for the histocompatibility swine system (SLA); Monoclonal antibodies and advances in molecular biology (Thacker 2003).

Immune Cells

White blood cells (leukocytes) are immune system cells that protect the body from infections and foreign substances. LaFleur-Brooks (2008) reported that five distinct types of leukocytes are produced from a multipotent cell in the hematopoietic stem cell. These white blood cells are present in the blood and lymphatic system (Maton *et al.*, 2008). Primary lymphoid organs are the bone marrow and thymus, which produce lymphocytes. Secondary lymphoid organs, such as lymph nodes and spleen, are where immune system cells fight off germs and foreign substances (IQWIG, 2023). In most species, lymphocytes enter secondary lymphoid organs via the blood, circulate within, and exit through lymphatic vessels if they do not encounter the appropriate antigens. However, in pigs, lymphocytes enter lymphoid organs through lymphatic vessels and exit directly into the blood (Thacker, 2004). All white blood cells share common characteristics but differ in form and function. One key distinction is the presence of granules in some leukocytes, dividing them into granulocytes and agranulocytes. Granulocytes (polymorphonuclear leukocytes) are identified by the varying staining granules in their cytoplasm when

observed under a light microscope. These granules contain enzymes enclosed in membranes that aid in digesting particles taken in by endocytosis. The three types of granulocytes are neutrophils, basophils, and eosinophils, named based on their staining properties (Sanchez-Vizcaino *et al.*, 1981; IQWIG, 2023).

Neutrophils are white blood cells that defend against bacterial or fungal infections and are the first responders to microbial infections. They are known as polymorphonuclear (PMN) leukocytes due to their multilobed nucleus. Neutrophils have a transparent cytoplasm with pale lilac granules and are highly active in phagocytosis. They play a crucial role in acute inflammation by killing foreign substances and make up 60-70% of the total leukocyte count. Neutrophils have a lifespan of about 8 days, and their death in large numbers contributes to the formation of pus (Sanchez-Vizcaino *et al.*, 1981; Pig333, 2017a).

Eosinophils are white blood cells that combat parasitic infections and are also the main inflammatory cells in allergic reactions. An increase in their levels may suggest allergies or parasitic infections. Their nucleus is typically bi-lobed, and their cytoplasm is rich in granules that take on a distinctive pink-orange hue with eosin stain (Sanchez-Vizcaino *et al.*, 1981).

Basophils play a key role in triggering allergic and antigen responses by releasing histamine, which causes inflammation. They have a bi- or tri-lobed nucleus that is often obscured by numerous coarse granules. Basophils are distinguished by their large blue granules (Sanchez-Vizcaino *et al.*, 1981). Agranulocytes, also known as mononuclear leukocytes, are white blood cells that lack visible granules in their cytoplasm. Despite the name suggesting no granules, these cells do possess non-specific azurophilic granules, which are lysosomes (Gartner and Hiatt, 2007). Examples are lymphocyte, monocyte and macrophage.

Lymphocytes are predominantly found in the lymphatic system. They are characterized by a deeply staining nucleus that may be eccentrically located, and have a relatively small amount of cytoplasm (Sanchez-Vizcaino *et al.*, 1981). The blood has three types of lymphocytes: B cells, T cells and cytotoxic T-cells. B cells produce antibodies that bind to pathogens, aiding in their elimination. In addition to producing antibodies, certain B cells can maintain the ability to

generate an antibody as a form of 'memory' following an infection. Immunoglobulins, also known as antibodies, are glycoproteins produced by B lymphocytes in response to antigens (Pig333, 2017b). They are secreted in body fluids and can bind to foreign pathogens to neutralise and eliminate them. These antibodies have a Y-shaped structure and play a key role in specific humoral immunity (Pig333, 2017b).

According to Takamatsu *et al.* (1999), the primary features of pathogenesis in domestic pigs infected with African swine fever virus (ASFV) are significant haemorrhage and B-cell apoptosis. Helper T cells (CD4+) play a crucial role in coordinating the immune response and defending against intracellular bacteria. During acute HIV infection, monitoring these T cells can indicate the individual's immune system activity. Saalmler (1998), and Sabir and Jan (2025) highlighted the Cytotoxic T cells (CD8+) can eliminate virus-infected and tumour cells. Studies suggest that CD8+ lymphocytes play a critical role in defending against African swine fever virus infection and the production of antibodies that target the virus. (Oura *et al.*, 2005). The $\gamma\delta$ T cells have a unique T cell receptor different from that of CD4+ and CD8+ $\alpha\beta$ T cells. They exhibit properties of helper T cells, cytotoxic T cells, and natural killer (NK) cells (Cano and Loper, 2013; Alspach *et al.*, 2019). Natural killer cells kill cells in the body which display a signal for destruction, once infected by a virus. Their activation and functions are regulated by both activating and inhibitory signals (Brandstadter and Yang, 2011).

Monocytes, which have a longer active life than neutrophils, perform phagocytic functions and present pathogen pieces to T cells for recognition and destruction. As monocytes leave the bloodstream, they transform into tissue macrophages that remove dead cell debris and attack microorganisms. Macrophages, with kidney-shaped nuclei and abundant cytoplasm, differentiate in the body tissues for the phagocytic activities (Sanchez-Vizcaino *et al.*, 1981). Fixed leukocytes migrate from the blood into the body tissues, where they take up permanent residence. These cells, such as the fixed macrophages in the liver known as Kupffer cells, play a role in the immune system even as they settle in specific tissues (Sanchez-Vizcaino *et al.*, 1981).

Major Histocompatibility Complex (MHC)

The major histocompatibility complex (MHC) is a cluster of genes that follows the Mendelian principle. They encode cell surface proteins. Their polymorphism determines graft acceptance or rejection (Janeway *et al.*, 2001). These genes help the immune system to differentiate between its own and foreign components. It plays a major role, not only in the immune response rejection of tissue grafts, but also in the antigen presentation and immune response development. Molecules codified by MHC genes bind to foreign proteins, labelling them so that the immune system can recognise and act against them (Sanchez-Vizcaino *et al.*, 1981; Janeway *et al.*, 2001). Every swine cell, except for erythrocytes, possesses certain surface proteins whose variations dictate whether grafted tissues will be rejected or accepted between different individuals. These proteins are part of the MHC in pigs and are referred to as Swine Leucocyte Antigens (SLA). It was first identified in 1970 (Vaiman *et al.*, 1970; Viza *et al.*, 1970), several decades after the identification of the mouse H-2 complex (Sanchez-Vizcaino *et al.*, 1981; Riberdy *et al.*, 1999; Sanchez-Vizcaino, 2006) and the human HLA (Human Leucocyte Antigen) system (Delves, 2024).

A correlation was identified between acute graft rejection and a group of surface antigens on peripheral lymphocytes. The genes encoding these antigens, known as SLA, are located on swine chromosome 7 and span approximately 2 Mb. Seventy of these genes have already been described by Sanchez-Vizcaino (2001). Ladowski *et al.* (2019) reported that human sera containing IgG specific for class II HLA molecules bind more effectively to cells positive for class II SLA than to those that are SLA negative. Sera lacking antibodies to class II HLA show no difference in binding, regardless of the presence of the SLA.

These antibodies can recognise SLA-DR or SLA-DQ complexes. Pigs, sharing a 98% genetic DNA similarity with humans, are among the closest mammals used in interspecies organ transplants, known as xenotransplants (<https://goodnewsplanet.com/how-much-dna-do-humans-share-with-other-animals-and-plants/>). Class II SLA proteins may act as xenoantigens for individuals with humoral immunity to class II HLA molecules

(Ladowski *et al.*, 2019). Similar to other animal species, pigs possess three distinct histocompatibility antigens, categorised by their chemical structure, tissue distribution, and function. These are referred to as Swine Leucocyte Antigens (SLA) classes I, II, and III. The antigens of classes I and II are protein molecules embedded in the cell membrane, featuring an extracellular region, a transmembrane segment, and a small cytoplasmic section. The class I and III antigens differ from class II antigens because they are located on opposite sides of the centromere of chromosome 7 (Geffrotin *et al.*, 1984; Rabin *et al.*, 1985; Nakamura *et al.*, 2019; Oluwole *et al.*, 2019; Hammer *et al.*, 2020), and they have a similar location to that of the human MHC (Matczyńska *et al.*, 2018; Hammer *et al.*, 2021).

Swine Leucocyte Antigen Complex Class I

Swine Leucocyte Antigen Genes Class I consist of classical and non-classical genes. Classical genes, which are part of the immunoglobulin gene family, play a role in presenting antigen peptides. Classical genes are present on the surface of all nucleated cells, except neurons and trophoblasts (Matczyńska *et al.*, 2018; Ando *et al.*, 2019; Oluwole *et al.*, 2019; Hammer *et al.*, 2021). During a viral infection, SLA I antigens are synthesised in the infected cells, where they bind to viral proteins, forming an SLA I-antigen complex. The SLA I-antigen complex is recognized by CD8+ cytotoxic T cells, which then kill the infected cells. One of the primary functions of SLA I is to present antigens to CD8+ T cells in infected cells (Vaiman *et al.*, 1988; Matczyńska *et al.*, 2018). The structure consists of two chains: a heavy chain, weighing 45 kDa (kilodaltons), known as the A chain, which is highly polymorphic and encoded by SLA genes. The light chain, known as the B polypeptide, weighs 11.7 kDa and is non-covalently linked to β 2-microglobulin. This light chain associates with the heavy chain, a transmembrane molecule within the SLA complex, exhibiting all the polymorphisms found in it (Vaiman *et al.*, 1998).

Innate Response against Viruses

Interferon and the activation of natural killer (NK) cells are key components of the innate immune response against viral infections, targeting and neutralising infected cells. Interferon, a cytokine, exists

in three distinct types, with the first two types mainly produced by monocytes-macrophages and, to a lesser extent, by fibroblasts. (Alberts *et al.*, 2002; Walker *et al.*, 2021). However, interferon is also produced by CD4⁺ and CD8⁺ lymphocytes, as well as NK cells. Interferon exhibits strong antiviral action and promotes various mechanisms, such as inducing temporary resistance in cells, stimulating the production of molecules with antiviral activity, activating genes that express antiviral proteins, and increasing the expression of SLA I and SLA II. NK cells are naturally activated against virus-infected cells, with their activation mechanism seemingly linked to changes in the SLA of the infected cells. Unlike T cells, NK cells do not rely on antigen recognition (they lack T cell receptors). This cytotoxic mechanism is highly effective in combating viral infections (Sanchez-Vizcaino *et al.*, 1981; Alpash *et al.*, 2019).

Adaptive Response against Viruses

Adaptive immunity combats viruses by targeting both the viral particles and the infected cells (Alberts *et al.*, 2002). Antibodies are the key defence mechanism against viral particles. The cytotoxic mechanisms, primarily mediated by CD8⁺ cells, antibodies, and the complement system (classical pathway), are crucial for attacking infected cells (Aristizabal and Gonzalez, 2013).

Viral Particle

The viral capsid, composed of proteins, is highly antigenic and stimulates the production of various antibodies (Lhomme *et al.*, 2021). These antibodies neutralise the virus (IgG, IgM, and IgA) by preventing its entry into cells and agglutinate the virus (IgM), reducing the number of infectious agents. Additionally, the antigen-antibody complex activates phagocytosis by stimulating the Fc receptor on macrophages (Sanchez-Vizcaino *et al.*, 1981). Cells infected by viruses can express on the membrane long before viral assembly occurs. Their destruction is an effective mechanism for preventing the production of more viruses. The adaptive immune response attacks infected cells using antibodies (ADCC system, classical pathway of complement activation, phagocytosis) and cytotoxicity mechanisms mediated by CD8⁺ lymphocytes. This is one of the most effective

mechanisms against viral infections (Sanchez-Vizcaino *et al.*, 1981). Researchers at the University of Cordoba delved into pigs' immune response in Porcine Reproductive and Respiratory Syndrome (PRRS) virus-infected lungs, highlighting Caspase-8's role in apoptosis, variation in lung macrophage populations, and key target cells for virus entry. They found that a decrease in macrophages leads to lung lesions and secondary infections. The research aimed at the production of vaccines despite the challenges of virus mutation (The Pig Site, 2024).

Genetics of Disease Resistance

Traditional genetic approaches have been used effectively in the swine industry to enhance feed efficiency, carcass leanness and reproductive traits. In the last decade, swine genome research has expanded from identifying genes associated with production and reproduction traits to swine health, well-being and disease-resistance traits (Lunney *et al.*, 2011). The ability of a host to resist infection can be referred to as resistance, while tolerance signifies a condition in which the host is infected by the pathogen but displays very limited adverse effects. If the breeding goal is to stop the spread of infection to another population, as with zoonoses, the resistance to a disease is far more advantageous than tolerance (Jovanović *et al.*, 2009). Disease resistance is the ability of an animal to resist disease when exposed to pathogens. Incorporating genetic elements into disease management strategies offers advantages, such as permanence of genetic change, broad-spectrum effects, and selection for increased resistance in the absence of infection (Azarpajouh, 2021).

Genetic investigations involving animal resistance to infections caused by pathogens of varying etiologies can be determined at three genetic levels: species, breed and individual animal genetic variation. The impact of genetic resistance to a disease-causing agent is greatest where all levels of genetic resistance act synergistically. When considering the significance of resistance/tolerance at the breed level, the intrinsic evolutionary advantage of breeds adapted to the environment should be uppermost. In tropical regions, where endemic diseases are widespread, due to their evolutionary roots, locally adapted autonomous breeds

display a far greater level of genetic resistance and adaptation than the imported breeds (Savic *et al*, 1995).

Individual variability and the identification of individuals whose resistance to disease can be determined through clinical examination or genetic markers (e.g. marker-assisted selection), which represents the first step in the formation of genetic resistance within a population. Depending upon disease etiology and the available animal genetic resources, the strategy for advancing genetic control of disease can be established through the following initiatives: the selection of locally adapted breeds, the implementation of cross-breeding methods geared at introducing genes significant in the expression of genetic resistance/tolerance towards pathogens, and the selection of individuals highly resistant to pathogens (Jovanović *et al.*, 2009).

Recovery from disease depends on an effective and protective immune response. Identifying genes that control immunity may help identify pigs with faster or better responses to disease challenges. Geneticists began addressing genetic disease resistance by assessing whether immune traits were highly heritable, then they mapped the genes involved referring to as the quantitative trait loci (QTL). These studies confirmed that the proportion of several blood immune cell subsets and serum antibody levels was heritable (Clapperton *et al.*, 2009). More recent efforts have affirmed that QTL for specific anti-disease antibody levels could be identified and mapped, along with the location of immune proteins associated with anti-disease responses (e.g., cytokines, such as anti-viral interferons). Other research established that a certain percentage of blood cell subsets correlate with improved growth rates throughout the entire productive life of the pig (Lunney *et al.*, 2011). Also, the RELA (v-rel avian reticuloendotheliosis viral oncogene homolog A) gene is associated with resistance to African swine fever virus (ASFv) infection, causing an overreaction in the immune system. Variations in RELA expression affect host response to ASF, as it is part of the NF-kappaB transcription factor involved in stress and immune defence.

Conclusion

The pig immune system is complex and similar to the human immune system, with little dissimilarity, where the pig MHC is located on 7 while the human is on 6 chromosomes. The innate immune response includes the complement system and various cell types like macrophages, neutrophils, basophils, mast cells, eosinophils, and natural killer cells. Identifying the classical (SLA1, 2 and 3) and non-classical (SLA 6,7 and 8) genes that control immunity in pigs can help in selecting animals that have faster or better responses to disease challenges. This can lead to improved overall health and productivity in pig populations. It is high time that awareness is raised that immunology, specifically vaccinology, can control many diseases in pigs, such as piglet diarrhoea, African swine fever, and porcine reproductive and respiratory syndrome (PRRS). The genes responsible for immune traits can be mapped using quantitative trait loci (QTL), in which genes specific to anti-disease antibody levels can be identified and mapped, along with the locations of immune proteins associated with anti-disease responses (cytokines).

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