UNIVERSITI PUTRA MALAYSIA

ROLES OF INTESTINAL INTRAEPITHELIAL LYMPHOCYTES IN SPECIFIC-PATHOGEN-FREE CHICKENS INFECTED WITH LENTOGENIC AND VELOGENIC NEWCASTLE DISEASE VIRUS STRAINS

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By

TASIU MALLAM HAMISU

Thesis Submitted to the School of Graduate Studies, Universiti Putra Malaysia, in Fulfilment of the Requirements for the Degree of Doctor of Philosophy

March 2021

DEDICATION

This thesis is dedicated in memory of my beloved parents. May God have mercy upon their departed souls, amen.

Abstract of thesis presented to the Senate of Universiti Putra Malaysia in fulfilment of the requirement for the degree of Doctor of Philosophy

ROLES OF INTESTINAL INTRAEPITHELIAL LYMPHOCYTES IN SPECIFIC-PATHOGEN-FREE CHICKENS INFECTED WITH LENTOGENIC AND VELOGENIC NEWCASTLE DISEASE VIRUS STRAINS

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March 2021

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There are increasing reports of Newcastle disease virus (NDV) shedding in vaccinated poultry flocks. Two intraepithelial lymphocytes (IEL), the Natural Killer (NK) cells and T cells, play a critical role in the control of virus shedding. The main objective of this study is to investigate the role of these cells in specific-pathogen-free (SPF) chickens following inoculation with NDV lentogenic strain LaSota, and/or velogenic strains, genotypes VII and VIII.

The SPF chickens were divided into groups of inoculated with lentogenic strain (LaSota); genotype VII (GVII); genotype VIII (GVIII); lentogenic and challenged with genotype VII (LSGVII); lentogenic and challenged with genotype VIII (LSGVIII); and the group of uninfected control. Immunophenotyping of NK and T cells subtypes was conducted using a flow cytometry. Furthermore, CD3-/CD25+/CD45+IEL NK cell was purified, and the expression profile of immune and apoptosis-related genes was quantified using Reverse Transcriptase Quantitative Polymerase Chain Reaction (RT-qPCR). Virus shedding was then measured using RT-qPCR. Data were analysed using Two-way Analysis of Variance(ANOVA).

The percentage of CD3+ cells showed a decreasing pattern in GVII and GVIII challenged groups compared with LSGVII and LSGVIII. Similarly, a steady decrease of CD3+/CD4+ cells in GVII and GVIII challenged groups was seen as the infection progressed. LSGVII and LSGVIII challenged groups, however, showed a statistically significant increase of these cells. A similar finding was obtained with CD3+/CD8+ cells.

Among all the experimental groups, the highest virus shedding occurred at 60 hrs post-challenge with GVII. There was a strong negative correlation between an increase in GVII shedding and a decrease in CD25+IEL NK cells. Following inoculation of LGVII, there was a statistically significant decrease in virus shedding in all the time points; however, there was no significant correlation between GVII shedding and CD25+IEL NK cells. There was no statistically significant difference in GVIII shedding between the time points of the GVIII challenge group and its corresponding LSGVIII group. There was a strong positive correlation between CD25+IEL NK cells and GVIII shedding in a LSGVIII challenged group.

The expression profiles of CD69, FasL and granzyme A, NK-lysin, and IFN-γ were generally upregulated in LSGVII and LSGVIII challenged groups. In contrast, B-NK, was downregulated. In NDV GVII and GVIII challenged groups, however, B-NK was upregulated, whereas the remaining receptors were generally downregulated except for CHIR-AB1.

Taking together, the findings of this study showed that CD25+IEL NK cell showed a strong negative correlation with GVII shedding, but no correlation with GVIII shedding. Furthermore, there was a moderate negative correlation between CD25+IEL NK cells and GVII shedding in LSGVII challenge group and a strong positive correlation between CD25+IEL NK and GVIII shedding in LSGVIII challenged chickens. The CD3-/CD25+/CD45+IEL NK cells in the LSGVII and LSGVIII showed enhanced NK cell activity through upregulation of the activating receptors, peptides and interferon-γ. In contrast, the function of CD3-/CD25+/CD45+IEL NK was downgraded through upregulation of inhibitory receptors following inoculation of GVII and GVIII NDV. In addition, enriched CD3-/CD25+/CD45+IEL NK cells may use both receptor and granules-mediated apoptosis pathways in killing virus-infected cells.

Abstrak tesis yang dikemukan kepada Senat Universiti Putra Malaysia sebagai memenuhi keperluan untuk ijazah Doktor Falsafah

PERANAN LIMFOSIT INTRAEPITELIAL USUS DALAM AYAM BEBAS-PATOGEN KHUSUS YANG DIJANGKITI VIRUS PENYAKIT NEWCASTLE STRAIN LENTOGENIKDAN VELOGENIK

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Terdapat peningkatan laporan peluruhan virus Penyakit Newcastle (NDV) pada flok unggas yang telah diberi vaksin. Dua limfosit intraepitelial, (IEL), iaitu sel Pemusnahan Semula jadi (NK) dan sel T, memainkan peranan yang kritikal dalam mengawal peluruhan virus. Kajian ini telah mengkaji peranan sel-sel ini dalam ayam yang bebas dari patogen khusus (SPF) setelah disuntik dengan strain lentogenik dan/atau velogenik NDV.

Ayam SPF ini dibahagikan kepada kumpulan yang disuntik dengan strain lentogenik (LaSota); genotip VII (GVII); genotip VIII (GVIII); lentogenik dan dicabar dengan genotip VII (LSGVII); lentogenik dan dicabar dengan genotip VIII (LSGVIII); dan kumpulan kawalan yang tidak dijangkiti. Imunofenotip subjenis sel NK dan sel T dijalankan dengan menggunakan sitometer aliran. Seterusnya sel CD3-/CD25+/CD45+IEL NK diperkaya, dan ekspresi profil gen yang berkaitan dengan imun and apoptosis dikuantifikasikan menggunakan Reverse Transcriptase Quantitative Polymerase Chain Reaction (RT-qPCR). Peluruhan virus seterusnya diukur menggunakan RT-qPCR. Data dianalisa menggunakan Two-way Analysis of Variance (ANOVA).

Peratusan sel CD3+ menunjukkan pola penurunan pada kumpulan yang dicabar oleh GVII dan GVIII apabila dibandingkan dengan LSGVII dan LSGVIII. Serupa juga, terdapat penurunan berterusan sel CD3+/CD4+ dalam kumpulan dicabar GVII dan GVIII semasa jangkitan berlangsung. Kumpulan dicabar LSGVII dan LSGVIII pula menunjukkan peningkatan sel yang menaik dengan signifikan secara statistik. Penemuan serupa juga telah diperolehi dengan sel CD3+/CD8+.

Dari kesemua kumpulan eksperimen tersebut, peluruhan virus paling tinggi berlaku 60 jam selepas dicabar dengan GVII. Terdapat korelasi negatif yang kuat antara kenaikan peluruhan GVII dan penurunan sel CD25+IEL NK. Berikutan suntikan LGVII, terdapat penurunan signifikan secara statistik bagi peluruhan virus pada semua titik masa; walaubagaimanapun, tidak ada korelasi signifikan antara peluruhan GVII dan CD25+IEL NK sel. Tidak ada perbezaan signifikan secara statistik bagi peluruhan GVIII antara titik masa pada kumpulan dicabar GVIII dan kumpulan LSGVIII sepadannya itu. Terdapat korelasi positif yang kuat antara sel CD25+IEL NK dan peluruhan GVIII dalam kumpulan LSGVIII yang di cabar.

Ekspresi profil bagi CD69, FasL, granzim A, NK-lysin, dan IFN-γ yang pada kebiasannya dikawalselia menaik dalam kumpulan dicabar LSGVII dan LSGVIII. Sebaliknya, B-NK telah dikawalselia menurun, kecuali bagi CHIR-AB1. Ekspresi profil reseptor ini, walaubagaimanapun, telah bervariasi dalam kumpulan LSGVII dan LSGVIII.

Kesimpulannya, dapatan kajian ini menunjukkan bahawa sel CD25+IEL NK menunjukkan korelasi negatif yang kuat dengan peluruhan GVII, tetapi tiada korelasi bagi peluruhan GVIII. Tambahan lagi, terdapat korelasi negatif yang sederhana antara sel CD25+IEL NK dan peluruhan GVIII pada ayam dicabar LSGVIII. Sel CD3-/CD25+/CD45+IEL NK pada LSGVIII dan LSGVIII melalui kawalselia menaik reseptor pengaktifan, peptida dan interferon-γ menunjukkan aktiviti sel NK yang dipertingkatkan. Disebaliknya, fungsi CD3-/CD25+/CD45+IEL NK diturunkan melalui kawalselia menaik reseptor perencatan berikutan suntikan GVII dan GVIII NDV. Tambahan juga, sel CD3-/CD25+/CD45+IEL NK yang diperkayakan boleh menggunakan kedua-dua reseptor dan laluan apoptosis berantarakan granul dalam membunuh sel yang dijangkiti virus.

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LIST OF ABBREVIATIONS

APC	Antigen Presenting Cells
APMV-1	Avian Paramyxovirus -1
AVMA	American Veterinary Medical Association
CD	Cluster of Differentiation
CMI	Cell-Mediated Immunity
CTL	Cytotoxic T lymphocyte
DTT	Dithiothreitol
DNA	Deoxyribonucleic Acid
ELD50	Mean Egg Lethal Dose
ELISA	Enzyme-Linked Immunosorbent Assay
FasL	Fas Ligand
F	Fusion Protein
FAO	Food and Agriculture Organisation
GAPDH	Glyceraldehyde-3-phosphate-dehydrogenase
GVII	Genotype VII
GVIII	Genotype VIII
HA	Haemagglutination
HAU	Haemagglutinating Unit
HI	Haemagglutinin Inhibition
HIV	Human Immunodeficiency Virus
HN	Haemagglutinin Neuraminidase
HVT	Herpesvirus of Turkeys
IACUC	Institutional Animal Care and Use Committee

IBV	Infectious Bronchitis Virus
IBDV	Infectious Bursal Disease Virus
IBS	Institute of Bioscience
IEL	Intraepithelial Lymphocytes
Interferon-γ	Interferon-gamma
Ig	Immunoglobulin
IHC	Immunohistochemistry
IL	Interleukin
L	Large Polymerase Protein
LSGVII	LaSota Inoculated-GVII Challenge
LSGVIII	LaSota Inoculated-GVIII Challenge
M	Matrix Protein
MHC-1	Major Histocompatibility Complex Class I
MHC-II	Major Histocompatibility Complex class II
ND	Newcastle Disease
NDV	Newcastle Disease Virus
ng/µL	Nanogram/microliter
NK	Natural Killer
vNDV	Velogenic Newcastle Disease virus
OIE	World Organisation for Animal Health
P	Phosphoprotein
PCR	Polymerase Chain Reaction
PBS	Phosphate Buffered Saline
PI	Post inoculation /Post infection
QPCR	Quantitative Polymerase Chain Reaction

RT-qPCR	Reverse Transcriptase Quantitative–PolymeraseChain Reaction
RNA	Ribonucleic Acid
rRNA	Ribosomal Ribonucleic Acid
RT-PCR	Real-Time Polymerase Chain Reaction
V	V protein
VRI	Veterinary Research Institute
W	W protein
WHO	World Health Organisation

CHAPTER 1

INTRODUCTION

1.1 Background of the Study

Newcastle Disease (ND) remains one of the important avian diseases affecting the poultry industry worldwide. The disease, together with highly pathogenic avian influenza (HPAI), formed the only List A poultry diseases considered severe enough by the Office Internationaldes Epizooties (OIE) (Alexander, 2000). Therefore, it represents oneof the major factors affecting the expansion of the poultry industry indifferent parts of the world. ND infects more than 200 wild birds andpoultry species (Miller & Koch, 2020). Among the avian species, chickens are more susceptible to ND; ducks showed no clinicalsymptoms, while waterfowls are natural reservoirs for the virus (Hines & Miller, 2012).

Newcastle Disease Virus (NDV), also called Avian *Orthoavulavirus 1* (AOAV-1), previously called *Avian Avulavirus* 1 (AAvV-1) (Dimitrov et al., 2019), is the causative agent of ND and has 20 serotypes (AAvV-1 to AAvV-20) (Miller & Koch, 2020). The virulent form of AAvV-1 has been the most significant poultry pathogen among all the other serotypes (Miller & Koch, 2020). The size of the NDV genome is approximately 15 kb nucleotides (Jin et al., 2016). The genome is pleomorphic with an enveloped negative- sense RNA consisting of six genes, that encode six proteins, which include: nucleocapsid protein (NP), phosphoprotein (P), matrix protein (M), fusion protein (F), hemagglutinin-neuraminidase protein(HN) and large polymerase protein (L) arranged in the order of 3'- NP-PM-F-HN-L-5'(Phale, 2018). Furthermore, two additional non-structural proteins, V and W, are encoded by *P* gen*e* (Jin et al., 2016).

The virus is transmitted through inhalation or ingestion of infected aerosol, feed/water (Samal, 2008). It affects the respiratory, gastrointestinal, nervous, and reproductive systems with a mortality rate of up to 100% in a non-vaccinated flock (Miller & Koch, 2020). Depending on the severity of clinical disease in chickens, NDV strains can be classified into three pathotypes: velogenic, mesogenic, and lentogenic strains. The velogenic strains are highly fatal (reaching 100% mortality), with clinical signs and lesions severely affecting the respiratory, gastrointestinal, and nervous system (Alexander & Jones,2008). On the other hand, the mesogenic strains are intermediate virulence, causing clinical illness in chickens characterised by moderate neurological and respiratory symptoms with low mortality.Meanwhile, lentogenic strains such as LaSota, V4, and Ulster strainsdo not usually cause notable clinical disease in adult chickens and areused as live vaccines (Brown et al., 1999).

One of the extensively studied physical barriers against invading pathogenic micro-organisms is the mucosa. NDV and many viruses also replicate first at the mucosal site; consequently, local immune responses are induced, thereby inhibiting the subsequent systemic infection by some of these viruses (Kagnoff, 1996; Bienenstock & Befus, 1980). Besides, the mucosa has been shown to play a critical role in adaptive immune responses (Neutra et al., 1996). The intestinaltract has long been described as the largest mucosal tissue and plays a significant role in the immunologic homeostasis of the body (MacDonald & Monteleone, 2005). The main site of the intestinal mucosal immune system is the gut-associated lymphoid tissue, whichcontained immune cells such as goblet cells, mast cells, intestinal intraepithelial lymphocytes (IEL) and secretory IgA (sIgA)-positive cells. The coordinated functions of these cells provide protection to the animal (DeWitt & Kudsk, 1999; Kagnoff, 1996).

Intraepithelial lymphocytes (IEL) provide the first line of immunological defense following the intestine invasion of apathogen. They perform several functions such as the production of certain cytokines, cytotoxic function and induce apoptosis in intestinal epithelial cells (Inagaki-Ohara et al., 1997; Yamamoto et al., 1994; Taguchi et al., 1991; Guy-Grand et al., 1991). Some components of innate immunity constitute part of IEL which providean immediate response.

The role of the innate immune system is not limited to scavenging andfighting invading micro-organism into the body but also includes pattern recognition and immune modulation, with a more significant role of crosstalk between different parts of the immune system (Juul-Madsen et al., 2013). The innate immune response of the host to virusinfection is immediate, aimed at retarding the growth of the virus so that the host can develop a specific immune response through adaptive immunity (Rue et al., 2011). The effect of NDV on the innateimmune response on chicken cells had been reported by several researchers.

One of the key players of innate immunity against virus infections is Natural Killer (NK) cells (Iannello et al., 2006). In chickens, up to 50% of the total NK cells are found in the intestinal epithelium (Göbel, 2000a). They exert their antiviral effect through the killing ofvirally infected cells at the early phase of infection. They also destroytransformed cells (Iannello et al., 2006). Furthermore, they facilitate crosstalk between innate and adaptive immunity by releasing certain cytokines such as IFN-γ, IL-15, TNF-α, and IL-22 (Abbas et al., 2010a). The NK cell functions are tightly regulated by two groups ofits surface receptors, the activating and inhibitory receptors (Vivier etal., 2008). The inhibitory receptors regulate NK cells biologicalfunction by recognizing major histocompatibility (MHC) molecules class I on the surface of the normal cells and subsequent inhibition of NK cell cytotoxic function. In virus-infected or transformed cells, however, the expression of MHC class I is rather downregulated. Consequently, the expression of inhibitory receptors is abrogated, while NK cell biological function is stimulated through activating receptors (Vivier et al., 2008). Similarly, the expression of some stressligands such as MHC complex class I chain A (MICA) on the surfaceof virus-infected cells can stimulate NK cell cytotoxic function through binding of NK cell-activating receptors with such ligands (Zwirner et al., 2006).

In addition to NK cells, T cells also constitute an arm of intestinal CMI. Unlike NK cells, T cells are a type of adaptive immune response. Functionally, T lymphocytes consist of two clearly distinguishable subpopulations that can be identified phenotypically based on their surface receptors, the T lymphocytes (CD8+), which recognize invading microorganisms based on MHC class I molecules, and helper T cells (CD4+), that recognize foreign antigens in the context of MHC class II molecules (Bucy et al., 1988). The majority of intestinal T lymphocyte subsets express CD3 polypeptides (gamma, delta, epsilon, and zeta) (Bucy et al., 1988).

1.2 Statement of the Research Problems

The outbreaks of genotype VII NDV in vaccinated farms had been reported from different parts of the world (Diel et al., 2012a; Berhanuet al., 2010; Rui et al., 2010; Jeon et al., 2008). In Malaysia, the indexfor reported outbreaks of Malaysia's genotype VII NDV showed an increasing trend in the past few years; from 5 outbreaks in 2009, to 75 and 153 outbreaks in 2010 and 2011, respectively (Department of Veterinary Services, Ministry of Agriculture, Malaysia (unpublisheddata). The cause of infection in vaccinated farms may be associated with several factors such as vaccination failure due to insufficient vaccine application, and antigenically heterologous vaccine (Hu et al., 2011). For instance, antigenically homologous vaccines were shown to prevent clinical symptoms against velogenic NDV challenge due to high systemic antibody levels (Reynolds & Maraqa, 2000a). Despite the high antibody titre, virus shedding continues to occur (Reynolds & Maraqa, 2000a). The ease of virus transmission amongstsusceptible birds may be facilitated by the presence of the virus in theenvironment. Consequently, there is renewed interest in the amount of NDV shed in the environment in an experimental lentogenic inoculated-velogenic challenge setting (Miller et al., 2009, 2007). Furthermore, antibody stimulation following challenge with NDV usually starts from one-week post-challenge (Kapczynski & King, 2005). Therefore, it would be interesting to investigate the role of thepresence of pre-existing immunity prior to generation of antibodies.

A recent study reported that specific-pathogen-free (SPF) chickens infected with Malaysian genotype VII and VIII have reduced numberof CD28-4+ IEL NK cells. In addition, these viruses generally downregulate CD3-/CD28-4+ IEL NK cell-activating receptors while upregulating CD3-/CD28-4+ IEL NK cell inhibitory receptors (Abdolmaleki et al., 2018). However, the relationship between IEL NK cells and genotype VII and VIII NDV shedding remains elusive. Furthermore, the role of lentogenic strain in chickens inoculated with lentogenic NDV and subsequently challenge with velogenic strain is yet to be investigated.

Previous study has reported a significant reduction in splenic Tlymphocytes population at 1 and 3 days following infection with genotype VII and VIII NDV (Rasoli et al., 2014). However, the population of IEL T cells following infection with genotype VII and VIII has not been reported. Besides, the role of lentogenic NDV in activating the T cell populations in lentogenic inoculated-velogenic challenge chickens has not been elucidated.

1.3 Hypotheses of the Research

1- There are increased in the population of CD25+IEL NK cells in LaSota inoculated-Genotype VII challenge (LSGVII) and LaSota inoculated-Genotype VIII challenged (LSGVIII) chickens when compared with chickens inoculated with Genotype VII (GVII) and Genotype VIII (GVIII);

2- There is an increase in the population of CD3+ IEL cell sub- types in LSGVII and LSGVIII inoculated chickens whencompared with chickens inoculated with GVII and GVIII;

3- The biological function of enriched CD3-/CD25+/CD45+IEL NK cells is enhanced in chickens inoculated with LSGVII andLSGVIII when compared with chickens inoculated with GVIIand GVIII;

4- Enriched CD3-/CD25+/CD45+IEL NK cells used bothreceptor and granules mediated apoptosis pathways. However, GVII and GVIII caused downregulation of these receptors, whereas LSGVII and LSGVIII caused upregulation of these receptors.

5- There is a correlation between CD25+IEL NK cells and virusshedding.

Therefore, this study aims to investigate the role of avian intestinal IEL in SPF chickens inoculated with lentogenic and velogenic strainsvia the following specific objectives:

1.4 Objectives

1) To identify the population of CD25+IEL NK cells following infection of SPF chickens with LaSota, LSGVII, LSGVIII, GVII and GVIII NDV strains;

2) To identify the population of CD3+IEL cell sub-types following infection of SPF chickens with LaSota, LSGVII, LSGVIII, GVII and GVIII NDV strains;

3) To measure the expression profiles of selected immune- related genes associated with enriched CD3-/CD25+/CD45+IEL NK cells following infection of SPF chickens with LaSota, LSGVII, LSGVIII, GVII and GVIII NDV strains;

4) To measure the expression profile of apoptosis-related genes that are associated with enriched CD3-/CD25+/CD45+IEL NK cells following infection of SPF chickens with LaSota, LSGVII, LSGVIII, GVII and GVIII NDV strains;

5) To investigate the correlation between virus shedding and CD25+IEL NK cell populations in SPF chickens inoculated with LaSota, LSGVII, LSGVIII, GVII and GVIII NDV strains.

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