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Editorial

Highlights of the 8th International Veterinary Immunology Symposium

1. The importance of veterinary immunology for immunobiology

The 8th International Veterinary Immunology Symposium was held on August 15th–19th, 2007, in Ouro Preto, Brazil. The symposium received 390 delegates from 30 countries and covered a wide range of research with a comprehensive program. The immune system of domestic and wild animals, how it is activated and regulated and how it performs its functions for defense against pathogens and stress and for reproduction were addressed in the context of genetics, endocrinology and nutrition. Veterinary immunology is not an endeavor which merely confirms in species of veterinary interest the knowledge generated in human or mice models. From Edward Jenner to Louis Pasteur, to Ray Owen and Bruce Glick, observations first made with domestic animals have provided the background for many groundbreaking discoveries in immunology and that went on to have lasting impacts on human as well as animal health. Comparative immunology, an essential topic in veterinary immunology, continues to shed light on evolution of the immune system. High levels of conservation of components of the innate immune system between invertebrates and vertebrates underscore the interfaces being discovered that affect the ability of the innate response to determine the outcome of the adaptive response. This conservation was highlighted by the Opening 8th IVIS lecture by J. Sharfstein, Brazil. He presented how bradykinin, a pro-inflammatory peptide generated by the kinin cascade and an innate danger signal, potently activates dendritic cells (DC) to generate Th1 profiles, pointing to a role for bradykinin as an adjuvant for vaccines.

Veterinary immunology offers many insights on strategies of immunity: cases in point are the interesting differences concerning the physiology of γδT cells and peripheral CD4+/CD8+ double positive T cells seen between, respectively, ruminants and swine and other species (Hein and Griebel, 2003). Studies in species of veterinary interest offer more relevant or complementary models than mice for studies of human immunology and infectious diseases. D.M. Estes, USA, pointed out that granulysin, one of the few proteins that reduces intracellular mycobacteria, is present in bovines and humans, but to date has not been identified in mice, nevertheless mice remain as the predominant animal model for development of anti-tuberculosis vaccines (Endsley et al., 2008). Kacskovics highlighted the crucial role for neonatal Fc receptor in IgG metabolism in livestock and humans (Cervenak and Kacskovics, 2008). K. Van Reeth, Belgium, uses the pig model for determining if immunity to H1N1 influenza can protect against an H5N1 avian influenza virus (AIV): post-infection immunity to H1N1 SIV confers partial cross-protection against challenge with a low pathogenic H5N1 AIV. Summerfield et al. (2008) probed the role of innate immune responses in controlling foot-and-mouth disease virus. A thought-provoking exercise comparatively analyzed genotypes of porcine, murine, and human immune system genes; the greatest similarity indices for NK cell, monocyte, macrophage, and dendritic cell phenotypes was found to be between swine and humans, whereas phenotypes and functions of T and B cells of mice were more similar to those of humans (H. Dawson, USA). John Butler, USA, pointed out that most models are wrong, some less than others, and the best model for a species is the species itself (Butler et al., 2008).

Several novelties of the bovine immune system were highlighted, including the phenotype of T regulatory (Treg) cells from bovine PBMCs; in an *in vitro* co-culture assay they do not function as such, suppression being mediated by IL-10-secreting CD14+ monocytes and WC1+ γδT cells (A. Hoek, The Netherlands). G. Bohach, USA, showed that a superantigen from *Staphylococcus* could induce T cells that have both the phenotype and function of Treg cells and suppress proliferation of naive T cells by means of IL-10 and TGF-((Seo et al., 2008). Other types of regulatory T cells were described by M. Jutila, USA, who employed a transcriptomic approach to characterize the functions of subsets of bovine γδT cells: CD8+ γδT cells have a regulatory phenotype, as reflected by expression of IL-10 and TGFβ, and a mucosal phenotype, as reflected by expression the adhesion molecule a4/b7, reflecting the need for tight regulation of the immune response in this tissue.

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Table 1
Key outcomes of the 8th IVIS.

- Broad use of technologies is revealing alternate approaches to identify infectious pathogens and plan control and prevention strategies.
- Transcriptomic and proteomic approaches are identifying underlying immune mechanisms controlling disease resistance and general immune responses for shrimp, pigs, cattle and chickens.
- Veterinary immune studies have highlighted a critical role for NK cells in innate immune responses.
- Improvements of delivery of antigen to professional antigen-presenting cells have enhanced the effectiveness of immune priming.
- Interactions of innate and acquired immune system have been exploited to improve anti-pathogen immunity and boost the efficacy of DNA vaccines and mucosal vaccination.
- Unique genes and proteins have been identified as critical factors for normal health and for prevention and control of diseases in animals; studies are beginning to reveal genetic polymorphisms in these genes that encode resistance or susceptibility to disease.
- Understanding the structure of camelid Ig genes has led to their use as biotherapeutics and nanobodies.

A. Stalker, United Kingdom (UK), showed that population lineage-negative cells that are phenotypically and functionally similar to plasmacytoid dendritic cells (pDCs) comprise an amazing 20% of the PBMCs in bovine blood, whereas in humans and mice this population is very small. The biological significance of these differences begs to be answered. Interestingly, pDCs traffic in intestinal lymph of bovines and ovines, while they are absent from intestinal and liver lymph in rodent models (D. Werling, UK). The roles of DC in swine pathogen responses and their application for clinical treatment of horses are reviewed here (McCullough et al., 2008; Steinbach et al., 2008). Regarding deficiencies of the immune system, D. Hickstein, USA, has bred litters of dogs bearing leukocyte adhesion deficiency, providing a useful resource for veterinary and human immunology. This was proven by the correction of the deficiency condition in four dogs with gene therapy using a foamy virus vector for the *CD18* gene, paving the way for treatment of this condition in humans.

2. Veterinary immunology and its role in animal health: immunity to pathogens and parasites and development of vaccines

Veterinary immunology serves as a crucial base for knowledge for generating new technologies for promoting healthier animals and safer food products. The report on the 6th IVIS (Lunney et al., 2002), held in 2001 in Uppsala, Sweden, noted veterinary immunology to be at that time "a particularly important topic, given the worldwide attention focused on the efforts to control foot-and-mouth disease (FMD), avian influenza and bovine transmissible spongiform encephalopathy (TSE), or "mad cow" disease, in farm animals". Six years later the distribution of themes for the invited talks and 290 posters exhibited at the 8th IVIS (summaries of which are published in this edition) reflects the fact that pathogens still mobilize the great majority of efforts in the field; more than half of the posters and of the invited talks contemplated pathogens and parasites and described mechanisms of immunity to them, efforts to develop immunological and genetically based methods for their diagnosis, control and prevention through novel vaccines. In fact, this has been the pattern of distribution of themes since the 1st IVIS, although the complexity of immune investigations has increased substantially. At the 8th IVIS scientists probed cell subset interactions not just in blood but in mucosal immune environments using an expanded array of monoclonal antibody (mAb) and molecular tools and functional genomic approaches. Table 1 provides a summary of Key Outcomes reported at this meeting.

Many speakers at the 8th IVIS presented results focused on immune responses to pathogens, including work on salmonellosis in birds (Chappell et al., 2008) and *Mycobacterium* in cattle macrophages (Harris et al., 2008; Sommer et al., 2008), in addition to alternate infection control mechanisms, e.g., β-glucans for *Escherichia coli* in pig (Stuyven et al., 2008). Prions were the focus of the talk by J. Richt, USA; disrupting the gene coding for the normal prion protein in cattle resulted in animals with normal physiology and, interestingly, less susceptibility to TSE. An equine α-defensin that binds to several gram-positive and negative bacteria and to a fungus was described by O. Bruhn, Germany, the first time that this component of innate immunity has been reported in a species of host other than primates, rodents and rabbits. Studies on the innate anti-viral protein APOBEC3G of primates, bovines and swine raise the intriguing possibility that it can thwart infections with endogenous as well as exogenous retrovirus (R. Harris, USA). IL-15, which stimulates production of TNF-α, is produced in a dysregulated, excessive fashion in malignant catarrhal fever (MCF), the first demonstration of this in a viral infection. This may explain the severe pathology of MCF seen in bovines, the unnatural host of the virus; however, treatment with the anti-TNF-α receptor mAb) did not ameliorate the disease outcome (D. Haig, UK).

The innate response of calves to *Babesia* depends on Natural Killer (NK) cells as the prominent population proliferating in spleen; NK/WC1$^-$/γδT cells are the major source of IFN-γ with splenic DC acting as regulatory cells and monocytes as effector cells (W. Goff, USA). This response is dependent on cell-to-cell contact, with engagement occurring in the red pulp of the spleen (R. Bastos, USA). NK cells can also act as primary responders and producers of IFN-γ in infections in bovine placenta with another protozoan, *Neospora caninum*; overactivated NK cells were predicted to be involved in abortion caused by infections with the parasite by P. Boysen, Norway. The developing importance of NK cells was highlighted by the pre-IVIS Veterinary Immunology Committee (VIC) workshop on the phenotype of NK cells in veterinary species.

The cytokine profile elicited by two of the most important microorganisms involved in bovine mastitis was compared; *E. coli* induces a more inflammatory-biased profile, with upregulation of IL-8, TNF-α and sustained activation of complement. Mastitis caused by *Staphylococcus aureus* presents with a diminished pro-inflammatory cytokine profile, thus D. Bannerman, USA proposed

that this may explain the tendency for this pathogen to establish chronic infection and that therapies that heighten the cow's inflammatory response to *S. aureus* may enhance clearance of the pathogen. The impact of oxidative stress on dairy cow health is discussed by Aitken and Sordillo (2008). Interaction between endothelial cells and *Haemophilus somnus*, the agent of bovine thrombotic meningoencephalitis, induces proinflammatory and procoagulative cytokines. The mechanism for this phenomenon was shown to be caused by phosphorylcholine, a component of the pathogen, that induces induce platelet aggregation and activation and increases expression of P-selectin, E-selectin, CD40L, FasL, and tissue factor (C. Czuprynski, USA).

Studies on immunity to blood-feeding ticks were more numerous than ever at the 8th IVIS. The dynamics of histamine release were shown to change during hematophagy: while the tick is attaching to the host, it inhibits histamine in order to escape from the inflammatory responses elicited by this mediator, but when the parasite reaches the stage of rapid feeding, histamine then comes in handy due to its ability to increase blood flow to the feeding site then HRF for rapid feeding phase. This sequential release into tick saliva depends on a histamine-binding protein followed by a histamine-releasing factor (A. Mulenga, USA). Another salivary component is involved in a more general tick escape mechanism: HeLIS, a protein of *Haemaphisalis longicornis*, decreases proliferation of bovine PBMCs and ConA-induced production of IL-2, Il-12 and TNF (M. Onuma, Japan). A vaccine against hookworm, another hematophagous parasite, is being developed using a canine model; a cocktail composed of antigens from the larval and adult stages of *Ancylostoma caninum* reduced both burdens of worms and blood loss in vaccinated dogs (A Loukas, Australia). Several authors discussed methods for understanding the pathology and potential control of canine visceral leishmaniasis during a special 8th IVIS mini-symposium (Bourdoiseau et al., 2008; de Andrade et al., 2008; Carrillo and Moreno, 2008; Reis et al., 2008).

As with past IVIS meetings vaccines and biotherapeutics were a major topic of the 8th IVIS. V. Gerdts, Canada, and P. Shewen, Canada, respectively, reviewed the importance of adjuvant design and mucosal vaccination (Garlapati et al., 2008; Shewen et al., 2008). A strategy to enhance efficacy of DNA vaccines was presented by W. Mwangi, USA, by directed priming of CD4+ and CD8+ T cells, recruiting DCs and targeting antigen to these cells with a DNA construct comprised of an anti-DEC205 scFv-antigen-CD40L chimera. Immunization of calves with the construct mixed with FLT3L/GM-CSF primed significant responses of IFN-(+ T cells. Improving delivery of antigen to professional antigen-presenting cells was the strategy described by J. Dominguez, Spain, who used a mAb recognizing porcine sialoadhesin to improve antigen presentation to T cells; targeting sialoadhesin increased production of antigen-specific antibodies. E.Y. Denkers, USA, demonstrated that $CD11c^{+}Gr\text{-}1^{+}$ splenic cells, displaying a phenotype consistent with pDC, are the target of infections with *Toxoplasma gondii* and inhibit their ability to produce IL-12; pDC thus turn into veritable "Trojan horses" for the infection. A similar population appears in the mesenteric lymph node (MLN) after oral infection.

3. Veterinary immunology and its role in animal health: impact of nutrients on immunity

The effect upon the immune response of components and deficiencies in the diet was an important topic at the 8th IVIS. J. Urban, USA, showed that deficiencies of vitamin E and selenium, known to hamper host protective responses to the helminth *Heligmosomoides polygyrus*, also interfere with intestinal expulsion of adult worms by means of mucus, intestinal motility induced by the cytokines IL-4 and IL-13 and activated macrophage killing of larvae via reactive oxygen species. Vitamin E also modulates the expression of Th2 cytokines by porcine PBMC, mainly through production of IL-10; data suggests that vitamin E preferentially increases expression of TBX21 over GATA3 (J. Hernández, México). Studies on the effect of probiotic bacteria *Bifidobacterium lactis* (Bb12) on the immune and intestinal function of swine were presented by H. Dawson, USA. High levels of Bb12 established in the large intestine induce changes in humoral immune response: following infection with *Ascaris suum* IgG1 and IgA antibody titers increase in the serum and intestinal fluid of probiotic-treated animals. Furthermore, Bb12 down-regulates the secretory responses to histamine, while maintaining baseline permeability and nutrient absorption it ameliorates the anti-absorptive effect of the nematode infection without impairing the host protective response, i.e., worm expulsion.

4. Veterinary immunology and reproduction

The mechanism of maternal immunotolerance of the semiallogeneic fetus has been a matter of intense investigation. The tryptophan-degrading enzyme indoleamine 2,3-dioxygenase (INDO) is reported to be critical because it generates Th2 polarizing kynunerins. J.R. Kfoury, Jr., Brazil, reported that progesterone, but not estrogen, increased INDO expression in cultured bovine placenta cells from first trimester; flow cytometry analysis confirmed the expression of INDO in bovine placenta throughout gestation. Pregnancy reduces production of IFN-γ, the cytokine which is associated with protection against *Clamydia*, and could explain susceptibility to *Clamydia* induced abortion in sheep. However, G. Entrican, UK, found no Th1 or Th2 cytokine biased response to antigen or mitogens in pregnant animals when compared to non-pregnant sheep.

5. Veterinary immunology and genetic and genomic studies of the immune system

The immune system encodes some of the most polymorphic genes of all the physiological systems, e.g., the major histocompatibility complex (MHC) genes. This most probably enables animals to deal with numerous pathogens, which present a huge diversity of foreign antigens as they establish themselves in hosts. Accordingly, immunogenetics was an important topic at the 8th

IVIS; a Comparative MHC Workshop was one of the pre-IVIS VIC activities. Comparisons of the genomic organization and polymorphisms of immune response genes of different species also raises interesting question about the biology of the products they encode; S. Ellis, UK, reported the large number of distinct receptors on bovine NK cells and that the complexity of these receptor was much greater than in mice and humans.

Large scale profiling of transcription of immune response genes in veterinary species was a feature of only a few presentations at the 7th IVIS; the 8th edition of the symposium saw a significant increase in work employing this approach. Many of the vaccine studies presented at the 8th IVIS employed transcriptomics to describe pathogens and discover new antigens and to track host responses. For this meeting it was planned that Dr. Jeanne Burton would give a presentation on the Neutrophil Transcriptome. Sadly Dr. Burton died within days of the 8th IVIS; a memorial tribute of Dr. Burton's career is included in this issue (Mallard et al., 2008). Transcriptomic studies in shrimp, pig and horses are reviewed in this volume (Dvorak et al., 2008; Lecoq et al., 2008; Robalino et al., 2008) as are proteomic studies of equine recurrent uveitis (Deeg, 2008). Numerous reports are now emerging of the importance of genetic polymorphisms in controlling disease responses and progression. W.E.R. Ollier, UK, demonstrated how the knowledge of the dog genome has enabled extensive analyses of genetic polymorphisms controlling canine diabetes mellitus highlighting the importance of cytokines in this autoimmune defect (Short et al., 2008).

A. Crawford, New Zealand, used transcriptional analyses with a 20,000 spot ovine cDNA microarray to interrogate expression of genes in duodenum tissue from nematode-resistant versus susceptible lambs. Limited numbers of differentially expressed genes were found between the resistant and susceptible animals, but at long times after infection. Up-regulation of class II MHC (DQA1) expression in some resistant sheep and may have a null allele in other. Overall these results will complement quantitative trait loci (QTL) searches for genes that mediate resistance to nematodes in sheep. J.K. Lunney, USA, used Affymetrix arrays to compare swine responses to the foodborne *Salmonella enterica* serovar Typhimurium (ST) versus the swine specific *S.* Choleraesuis (SC). By analyzing early responses (8, 24 and 48 h post-inoculation) and using bioinformatic approaches she and colleagues were able to demonstrate differential activation of 2365 differentially expressed genes many of which were found to be NFkB regulated transcription factors. Work comparing the gene expression profiles of extraembryonic tissue (ET) and embryonic disks (ED) derived from artificial insemination (AI) and somatic cell nuclear transfer (SCNT) showed that, of over 9000 genes were differentially expressed between ET and ED, 136 coded for proteins involved in immune functions including TLR3, 4, 6 and 9, TGFB1, DRA, TNF, IL6R, and IL1B; among the 188 genes differentially expressed by ET derived from different strategies employed for development of embryos (AI and SCNT) several also were also immune function genes, including TLR4, CD96, CD79B (H. Lewin, USA). T. Niewold, Belgium, examined the *in vivo* intestinal transcriptional response to rotavirus infection in germ-free piglets. When compared with resulted from infected Caco2 cells very few genes exhibited altered expression in jejunal tissue; those in common included GBP2, PAP and IFABP.

Participants also learned how a classical genetic approach can be exploited to identify protective antigens against the protozoan pathogen, *Eimeria maxima*. Two strains of this parasite, one of which is drug-resistant, were used to infect avian hosts, in which they sexually recombined. The progeny of these crosses were then used to infect drug-treated hosts that also presented strong immunity to one, but not to the other of the parental strains. These two simultaneous barriers selected and killed the parental genotypes; the recombinant parasite does not express the molecular mediators that promote infection and that should represent relevant antigens. A. Smith, UK, is now in the process of comparing genetic markers present on the parasites that survived this double barrier with those of the parental strains, of unselected progeny of the cross, and of single-barrier selected populations in order to reveal genomic regions that may code for relevant antigens. It will be exciting to see what genes this approach will identify.

D. Werling, UK, presented an interesting strategy for promoting resistance to disease in livestock: target the innate immune system by marker-assisted selection of animals bearing non-synonymous single nucleotide polymorphisms (SNPs) of toll-like receptors. These SNPs, in turn, are selected based on their functional consequences of either hyper- or hypo-responsiveness to bacterial products or infection, depending on the specific situation. This strategy could also take into consideration the prevalence of infections in different productive situations, such as bovine tuberculosis in dairy cattle.

6. Wind in the sails of veterinary immunology

Farm animals are important sources of high quality protein and are the livelihood of many. All animals are sources of zoonoses. Current production systems of farm animals impact their immune responses; high biosecurity helps to prevent new zoonoses. Veterinary immunologists have expanded understanding of the immune systems for our companion animals and developed new vaccines and therapeutics. Species of veterinary interest can clearly be better models for human disease than the mouse, as each species relies on different immune strategies to control pathogens and veterinary species are evolutionarily closer to humans. These situations underscore the fundamental role of veterinary immunology in promoting knowledge, human and animal health and improved production systems.

In spite of the demands, the number of scientists working in veterinary immunology is relatively small. If more advances have not been achieved and more diseases conquered at this point an examination of priorities in funding, including funding for development of immunological reagents for veterinary species, must be undertaken. As addressed in all the previous IVIS meetings and in the pre-8th IVIS VIC Toolkit Workshop, the availability of immunological reagents specific for species of veterinary interest still lags behind the demand and what is available for human and mouse immunology. The advances in genomics has only

Table 2
Challenges and opportunities for veterinary immunology today.

- Investments in basic investigations of species immunology will substantially improve knowledge of animal health and will be essential to improve disease prevention and to aid vaccine developments in veterinary species.
- Use of genomic information will improve comparative immunological studies and highlight the role of veterinary species as human health and disease models.
- Probes of how the immune system works at the host–pathogen interface are essential and will lead to an understanding of why certain interactions are species specific but not all?
- Future studies will transform genome information from both host and pathogens into products for better health and improved food productions systems.
- Developments are dependent on the immune toolkit; without expansion of available immunoreagents for each veterinary species investigations will be curtailed.

partly ameliorated this problem because, despite the availability of extensive nucleotide sequences and expression data, this information still does not substitute for detection of proteins as a means for obtaining as complete a phenotype for cellular populations and interactions. Genomic technologies probably will never be able to determine the place of specific cell populations and immune biomarkers in the architecture and organization of cellular reactions to danger signals. In a way, the community of veterinary immunologists is fortunate that this is a problem that money can solve. The article presented by Entrican et al. (2008) shows how toolkit resources have increased and where they are still needed. Yet the potential is enormous; as an example, the developments in understanding the single chain camelid immunoglobulins have set the stage for their extensive use as biotherapeutics and for nanobody technology (Muyldermans et al., 2008). Table 2 provides a short summary of Challenges and Opportunities for Veterinary Immunology today.

7. Awards and acknowledgments

It was gratifying to see that over one forth of the participants were graduate students, six of whom received awards for their poster presentations: Matt A. Firth (University of Guelph, Canada) for his discovery of novel receptors for IgG Fc on bovine lymphocytes; Jesse Thomas (CSIRO Livestock Industries, Australia) for his work showing that chicken IL-12 induces expression of the IL-18 receptor and, together with IL-18, also synergistically stimulates production of IFN-γ; Daniela Dantas Moré (University of São Paulo, Brazil) for her work showing that tick infestations affect subpopulations of peripheral blood lymphocytes; Agustin Ostachuk (Instituto Nacional de Tecnología Agropecuaria, Argentina) for developing a novel strategy for increasing immunogenicity of E2 glycoprotein (E2T) from BVDV by directing it to antigen presenting cells; Kathryn MacKinnon (Virginia Tech, USA) for her work that determined the differences in expression of immune response genes between *Haemonchus contortus*-resistant hair and susceptible wool lambs; and Sandra Regina Costa Maruyama (University of São Paulo, Brazil) for her work that employed transcriptomes of ticks fed on resistant and susceptible cattle to identify parasite genes affected by host immune responses. These awards were made possible by funds donated by the 7th and 8th IVISs. The chairs of the 8th IVIS congratulate the students and thank the members of the Student Poster Evaluation Committee, Ana Paula Junqueira-Kipnis, David Artis, Ildiko van Rhijn, Isabelle Oswald, Joan K. Lunney, Juan Anguita, Maristela Martins Camargo, Preben Boysen, Ricardo Fujiwara, Waithaka Mwangi and Rosangela Zacarias Machado, for their critical judgments. The Veterinary Immunology Committee of the International Union Immunological Societies Pfizer Distinguished Veterinary Immunologist Award was granted to Dr. John Butler, USA, for his work towards understanding the biology of immunoglobulins and their diversity in terms of variable, antigen recognition regions and constant regions in different species of animals (Butler et al., 2008).

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Conflict of interest

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