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Relevance of bovine tuberculosis research to the understanding of human disease: Historical perspectives, approaches, and immunologic mechanisms

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ABSTRACT

Pioneer studies on infectious disease and immunology by Jenner, Pasteur, Koch, Von Behring, Nocard, Roux, and Ehrlich forged a path for the dual-purpose with dual benefit approach, demonstrating a profound relevance of veterinary studies for biomedical applications. Tuberculosis (TB), primarily due to *Mycobacterium tuberculosis* in humans and *Mycobacterium bovis* in cattle, is an exemplary model for the demonstration of this concept. Early studies with cattle were instrumental in the development of the use of Koch's tuberculin as an *in vivo* measure of cell-mediated immunity for diagnostic purposes. Calmette and Guerin demonstrated the efficacy of an attenuated *M. bovis* strain (BCG) in cattle prior to use of this vaccine in humans. The interferon-γ release assay, now widely used for TB diagnosis in humans, was developed circa 1990 for use in the Australian bovine TB eradication program. More recently, *M. bovis* infection and vaccine efficacy studies with cattle have demonstrated a correlation of vaccine-elicited T cell central memory (T_{CM}) responses to vaccine efficacy, correlation of specific antibody to mycobacterial burden and lesion severity, and detection of antigen-specific IL-17 responses to vaccination and infection. Additionally, positive prognostic indicators of bovine TB vaccine efficacy (i.e., responses measured after infection) include: reduced antigen-specific IFN-γ, iNOS, IL-4, and MIP1-α responses; reduced antigen-specific expansion of $CD4^+$ T cells; and a diminished activation profile on T cells within antigen stimulated cultures. Delayed type hypersensitivity and IFN-γ responses correlate with infection but do not necessarily correlate with lesion severity whereas antibody responses generally correlate with lesion severity. Recently, serologic tests have emerged for the detection of tuberculous animals, particularly elephants, captive cervids, and camelids. B cell aggregates are consistently detected within tuberculous lesions of humans, cattle, mice and various other species, suggesting a role for B cells in the immunopathogenesis of TB. Comparative immunology studies including partnerships of researchers with veterinary and medical perspectives will continue to provide mutual benefit to TB research in both man and animals.

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1. Introduction: historical perspectives to the one health approach

The dual purpose with dual benefit (One Health) approach originated with the onset of research into the characterization of etiologic agents for infectious diseases, associated preventive strategies (i.e., vaccines), and the immune response elicited by the agents. For instance, the principle of vaccination was developed through insightful observations and experimental studies of Edward Jenner and others on the cross protective nature of cowpox for small pox in humans. Robert Koch and Louis Pasteur, co-founders of medical microbiology, each worked extensively on diseases of veterinary and biomedical importance. Koch discovered the etiology of anthrax by inoculating sheep with blood from infected animals while Pasteur produced the first live attenuated (laboratory produced) bacterial vaccine for fowl cholera as well as an effective anthrax vaccine for cattle. The Spanish physician, Jaime Ferrán, worked on veterinary vaccines prior to developing the first vaccine for immunizing humans against a bacterial disease—cholera. With his earnings from the 1st Nobel Prize in Medicine and Physiology for the serum theory with diptheria and tetanus (von Behring, 1901), Emil Von Behring switched the focus of his work almost exclusively to the development of a vaccine for tuberculosis (TB) in cattle using chemically inactivated *M. tb* complex strains (e.g., Tuberkulase and Taurovaccine) or human-derived tubercle bacilli attenuated by lengthy propagation (designated Bovovaccine) (reviewed in Linton, 2005). Concurrent with Behring's studies, McFadyean and colleagues in England and Pearson and Gilliland in the United States each demonstrated protective effects of live *M. tb* vaccination against experimental *M. bovis* infection in cattle (Flexner, 1908). This cross-protective strategy was abandoned, however, due to obvious safety concerns and variability in virulence of the human tubercle bacilli in cattle. Use of *M. tb* for vaccination of cattle against bovine TB, however, did establish a precedent followed by Albert Calmette and Camille Guerin in their development of an attenuated *M. bovis* (bacillus of Calmette and Guerin, BCG) for eventual use as a vaccine in cattle, humans, and various other species (Fine, 1995; Waters et al., 2012a).

Research efforts on bovine and human TB have been intimately linked beginning as early as the seminal studies on the etiology and pathogenesis of TB performed by Koch, Jean Antoine Villemin, and others in the mid to late 1800s (Palmer and Waters, 2011). Initially, Koch postulated that the tubercle bacilli from cattle and human were identical, dismissing the studies of Villemin that demonstrated a greater virulence of bovine-origin versus human-origin isolates in rabbits. Later, studies by Theobald Smith, a physician scientist working for the Veterinary Division of the Bureau of Animal Industry, demonstrated definitive differences between the bovine and human isolates based upon variable virulence of the two isolates in cattle, rabbits and guinea pigs; as well as morphological differences and differential growth characteristics of the two organisms on glycerin media. In addition to these contributions, veterinary researchers developed essential tools for the control of bovine TB that were concurrently or later adapted for use in the control of human TB. These include: (1) studies demonstrating the safety and efficacy of BCG (including demonstration that booster doses are generally not beneficial), (2) use of tuberculin as an *in vivo* diagnostic reagent, and (3) development of interferon (IFN)-γ release assays (IGRA) for diagnosis. In 1913 at the Pasteur Institute (Lille, France), Calmette and Guerin vaccinated 9 cows with *M. bovis* (Nocard strain, Edmond Nocard was Guerin's mentor) attenuated by serial passage on glycerol soaked potato slices in ox bile (i.e., BCG) (Calmette and Guerin, 1911). All 9 animals were protected from challenge with virulent *M. bovis*; thereby, demonstrating the potential use of BCG vaccination against *M. tb* infection of humans. In 1921, BCG was administered to a newborn child (6 mg orally) and has since been used widely by various administration routes for the control of human TB. Within a few years of the discovery of tuberculin by Koch, veterinary investigators in Russia (Professor Gutman), the UK (John McFadyean), Denmark (Bernhard Bang), and the US (Leonard Pearson and Maz'yck Ravenel) began using tuberculin as an *in vivo* diagnostic reagent for TB in cattle (Marshall, 1932). Clemens von Pirquet and Charles Mantoux later (circa 1907/1908) adapted and improved this technology for use in humans, coincidently defining the principles of allergy and delayed type hypersensitivity (DTH). During the 1980s, an IGRA was developed in Australia by Paul Wood, Leigh Corner, James Rothel, Stephen Jones, and others for the diagnosis of TB in cattle (Wood et al., 1990); a modified version of this assay is now widely used in the diagnosis of both human and bovine TB. Most recently, recombinant proteins and peptide cocktails of early secretory antigenic target-6 (ESAT-6), culture filtrate protein 10 (CFP-10), and various other antigens are in use with IGRA's (reviewed in Vordermeier, 2010; Vordermeier et al., 2011a,b) and in development for use as skin test antigens in cattle to improve specificity over purified protein derivative (PPD) preparations and as DIVA (differentiate infected from vaccinated animals) reagents (Whelan et al., 2010a,b,c). Field studies with cattle will prove invaluable for the eventual application of similar DIVA strategies for use in the control of human TB. Undoubtedly, advances in basic immunology, antigen discovery, comparative mycobacteriology, and vaccine approaches for human TB using animal models and clinical trials in humans have advanced research efforts on bovine TB. Together, co-discovery in TB research using both veterinary and biomedical approaches is an exemplary model of the one health concept.

2. Etiology, control measures and experimental biology approaches

2.1. Etiology and epidemiology

Tuberculosis in animals and humans may result from exposure to bacilli within the *M. tb* complex (i.e., *M. tuberculosis, M. bovis, M. africanum, M. pinnipedii, M. microti, M. caprae*, or *M. canetti*) (Cousins et al., 2003). *Mycobacterium bovis* is the species most often isolated from tuberculous cattle. Significant reservoirs exist for bovine TB (i.e., *M. bovis*) including white-tailed deer (*Odocoileus virginianus*, United States), Eurasian Badgers (*Meles meles*, United

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