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ABBREVIATIONS

The following abbreviations may be used without definition in *Poultry Science*. Plural abbreviations do not require "s". Chemical symbols and three-letter abbreviations for amino acids do not need definition. Units of measure, except those shown below, should be abbreviated as listed in the *CRC Handbook for Chemistry and Physics* (CRC Press, 2000 Corporate Blvd., Boca Raton, FL 33431) and do not need to be defined.

AME apparent metabolizable energy MHC major histocompatability complex AMEn nitrogen-corrected apparent mRNA messenger ribonucleic acid MNOVA analysis of variance mo month B cell bursal-derived, bursal-equivalent MS mean square derived cell N normal normal bp base pairs n number of observations BSA bovine serum albumin NRC National Research Council BW body weight NS not significant C cytosine PAGE polyacrylamide gel electrophoresis cDNA complementary DNA PBS phosphate-buffered saline cfu colony-forming units ppm parts per million CP crude protein pfu plaque-forming units cpm coefficient of variation r² coefficient of determination, simple dd day R² coefficient of determination, multiple df degrees of freedom RIA ratoiomunoassay DM dryme-linked immunosorbent s.c. subutance acid g grant SDS socium dodecyl sulfate g gravity SE standard error	A	adenine	MEn	nitrogen-corrected metabolizable energy
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M molar wk week ME metabolizable energy x mean yr year	μ	micro	wt/wt	weight to weight
ME metabolizable energy x mean yr year	М	molar	wk	week
vr year	ME	metabolizable energy	x	mean
			yr	year

*Also capitalized with any combination, e.g., mL.

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T Cell Development in the Chicken¹

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ABSTRACT This review summarizes our current view of $\gamma\delta$ and $\alpha\beta$ T cell development in the chicken. In it we emphasize the functional interplay between the $\gamma\delta$ and $\alpha\beta$ T cell subpopulations.

(*Key words*: T cell receptors $\gamma \delta$ and $\alpha \beta$, V β usage, T cell subpopulations, accessory molecules, monoclonal antibodies)

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INTRODUCTION

Many features of T cell development in birds and mammals are very similar. The T cell receptors (TCR) and accessory molecules defined for mammalian T cells are well conserved in birds. The analysis of avian T cell development using monoclonal antibodies against these cell surface molecules also reveals that the central features of T cell development in mammals are also conserved in the chicken. On the other hand, the avian T cell repertoire is much less complex, and the avian embryo more assessible for experimental manipulation. These and other unique features make the avian model system an informative one for study of T cell development and function.

T CELL RECEPTORS AND ACCESSORY MOLECULES

Monoclonal antibodies (mAb) have been produced against a variety of functionally important molecules expressed on the surface of chicken T cells (Chen et al., 1991), and most of these have well-defined mammalian counterparts. The chicken T cell receptors can be divided into three subgroups, each of which can be identified by a specific mAb. All of the $\gamma\delta$ T cells are recognized by the TCR1 mAb (Sowder et al., 1988), whereas two discrete subsets of $\alpha\beta$ T cells can be identified by the TCR2 and TCR3 mAb (Chen et al., 1988; Cihak et al., 1988; Char et al., 1990). All three receptor molecules are disulfide-linked heterodimers that are noncovalently associated with a CD3 protein complex to form a signal transduction unit. The avian CD3 complex contains chains similar to the mammalian CD3 γ , δ , ϵ , and ζ chains (Chen et al., 1986; Göbel et al., unpublished data), but only the CD3 gene that encodes a 19-kDa chain has been cloned so far (Bernot and Auffray, 1991; Lahti et al., St. Jude Children's Research Hospital, Memphis, TN 38101-0318, personal communication). The sequence of this chicken CD3 protein has homology with both the mammalian CD3 γ and δ chains.

The CD4 and CD8 coreceptors have also been identified in the chicken (Chan *et al.*, 1988). The CD4 molecule is a single peptide and CD8 is a disulfide-linked dimer. Each molecule is associated with a cellular tyrosine protein kinase that is homologous to the mammalian p56^{lck} (Veillette and Ratcliffe, 1991). As in mammals, both CD8 α and β chains are expressed in the chicken to form CD8 $\alpha\alpha$ homodimers and CD8 $\alpha\beta$ heterodimers

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(Kong et al., 1994; Young et al., Institute for Animal Health, Newsbury, Berkshire RG16 ONM, U.K., personal communication). The molecular weights, tissue distribution, and function of the TCR/CD3, CD4, and CD8 molecules are all very similar to their mammalian counterparts (Chen et al., 1990; Cooper et al., 1991).

THREE SUBPOPULATIONS OF T CELLS

The avian thymus is colonized with thymocyte precursors in waves during embryogenesis, and the thymocyte progeny of each sequential wave overlap each other (Coltey et al., 1987). During T cell ontogeny, the three subpopulations of T cells appear in the order TCR1, TCR2, and TCR3 (Char et al., 1990). Analyses of chicken thymocyte development in chickquail chimeras reveal that all three subsets of T cells are derived from each wave of thymocyte precursors (Coltey et al., 1989). Migration of the three T cell subsets to the periphery also follows the same TCR1, TCR2, an TCR3 order (Char et al., 1990), but the TCR2 cells become the predominant population in mature chickens.

UNIQUE FEATURES OF TCR1 ($\gamma\delta$) CELLS

Unlike human and mouse, in which $\gamma\delta$ cells comprise a minor subset of T lymphocytes in the circulation (Haas *et al.*, 1993), the chicken has a relatively large subset of $\gamma\delta$ T cells (Sowder *et al.*, 1988). The frequency of TCR1 cells is usually 20 to 25% of the total blood T cells, but can reach approximately 50% in chickens of 6 mo of age (Cihak *et al.*, 1993). The high frequency of avian $\gamma\delta$ T cells and the availability of the anti- $\gamma\delta$ mAb has allowed extensive characterization of the properties of $\gamma\delta$ T cells in the chicken (Table 1).

The $\gamma\delta$ thymocytes are unlike the $\alpha\beta$ T cells in that they express high levels of their TCR complex from the earliest time in appearance in the thymic cortex, and these $\gamma\delta$ receptors are relatively difficult to modulate by receptor cross-linkage (George and Cooper, 1990). Whereas $\alpha\beta$ thymocytes take several days to migrate

TABLE	1.	Special	f	eatures	8 0	f avia	n
Тce	ll r	eceptor	1	(TCR	1)	cells	

1.	Large subpopulation of T cells
2.	Characteristic intrathymic developmental pattern
	Short cortical transit time
	High level of TCR1/CD3 expression
	Not easily aborted via TCR1-mediated signals
3.	Preferential homing to intestinal epithelium and splenic red pulp
1	Acquire CD8 in the periphery

- Acquire CD8 in the periphery
 Cytotoxic capability, but lack graft-vs-host potential
- 6. Require exogenous growth factors

from cortex to medulla, during which they undergo extensive proliferation and selection, $\gamma\delta$ cells rapidly traverse this compartment and soon exit from the thymus (Bucy *et al.*, 1990). These results suggest that $\gamma\delta$ T cells may not undergo the same selection pressures as $\alpha\beta$ thymocytes.

The distribution patterns differ for $\alpha\beta$ and $\gamma\delta$ cells in peripheral lymphoid tissues (Bucy *et al.*, 1988). In the spleen, the $\gamma\delta$ cells are located predominantly in the sinusoidal areas. In the intestine, they are preferentially localized in the epithelium. In contrast, both TCR2 and TCR3 cells home to the periarteriolar lymphatic sheaths in spleen, and TCR2 cells are located mainly in the lamina propria of the intestine. Interestingly, TCR3 cells are rarely found in the intestine.

The majority of the $\gamma\delta$ cells in thymus and blood are CD4-CD8- (Sowder *et al.*, 1988), although a small subset of them may express CD8 or CD4 coreceptors (unpublished data; Davidson *et al.*, 1992). However, when the $\gamma\delta$ cells migrate into the spleen and intestine, most of them begin to express CD8.

The biological function of $\gamma\delta$ T cells is still unclear, but they are clearly capable of cytotoxic activity *in vitro*. Using a redirected cytotoxicity assay, $\gamma\delta$ T cells were shown to specifically lyse anti-CD3 hybridoma cells (Chan *et al.*, Rutgers University, Piscataway, NJ 08855-6268, personal communication). The CD8+ $\gamma\delta$ T cells may also be involved in downregulation of immune responses (Quere *et al.*, 1990). However, they are incapable of inducing graft-vs-host (GVH) reactions, whereas both the TCR2 and TCR3 subpopulations of CD4+ $\alpha\beta$ T cells are capable of GVH activity (Char *et al.*, Baylor College of Medicine, Division of Neurosciences, Houston, TX 77030-3498, personal communication).

DEPENDENCE OF $\gamma \delta$ T CELL GROWTH ON $\alpha \beta$ T CELLS

During studies on the developmental origin of $\gamma\delta$ T cells, we examined the longterm effects of thymectomy on the development of T cells. Neonatal thymectomy resulted in a dramatic and persistent decrease of TCR1 cells to a frequency of 5% or less of blood T cells, whereas the frequencies of TCR2 and TCR3 cells were not altered significantly (Chen et al., 1989; Cihak et al., 1993). This observation suggests that expansion of the $\gamma\delta$ population in the periphery requires continual seeding of thymic $\gamma\delta$ T cells. Moreover, unlike the $\alpha\beta$ cells that exhibit follicular growth, $\gamma\delta$ cells do not. Instead they are randomly distributed in the peripheral tissues predominantly as single cells (Bucy et al., 1990). These results imply that the $\gamma\delta$ T cells differ strikingly from $\alpha\beta$ T cells in their proliferative characteristics.

Because of their high frequency in the chicken, it is relatively easy to analyze the growth requirements of normal $\gamma\delta$ T cells. When TCR1, TCR2, and TCR3 cells are purified by negative selection and their proliferative responses compared, the TCR1 cells cannot respond well to mitogens or TCR ligation, except in the

presence of $\alpha\beta$ T cells. In contrast, the $\alpha\beta$ T cells can grow very well alone (Kasahara et al., 1993). The TCR1 cells fail to produce adequate amount of interleukin (IL)-2 and they proliferate in response to receptor ligation only in the presence of exogenous cytokines, including IL-2. Furthermore, only the CD8+ subpopulation of $\gamma\delta$ T cells responds to the dual stimulation of receptor ligation and exogenous growth factors. The CD8+ $\gamma\delta$ T cells are relatively large and express MHC Class II on their surface, indicating a state of activation. Because activated T cells can process and present antigen (Wyss-Coray et al., 1993), we suggest that a two-way interaction between $\gamma\delta$ and $\alpha\beta$ T cells may result in mutual regulatory roles of these two subpopulations in the immune response (Kasahara et al., 1993). Analysis of this interaction may be essential for understanding the biological function of $\gamma\delta$ T cells.

TWO DISTINCT SUBPOPULATIONS OF $\alpha\beta$ T CELLS

TCR2 and TCR3 Cells Differ in Function

In addition to their differences in ontogeny and tissue distribution, the two $\alpha\beta$ T cell subpopulations that express TCR2 or TCR3 receptors also exhibit functional differences (Table 2). Both TCR2 and TCR3 cells are capable of GVH alloreactivity, but they vary in their GVH potential depending on donor and recipient MHC combinations

Variable	TCRα	TCRβ
cDNA, kb	1.7	1.3
Amino acids	257	273
Predicted molecular weight, kDa	28	31
Predicted isoelectric point	5.0	8.5
Possible N-glycosylation sites	1	4
Homology to mammals, %		
Constant region	26	35
Joining region	35	47
Diversity region	1	+
Variable region	28	22 (Vβ1) 46 (Vβ2)

TABLE 2. Comparison of chicken T cell receptor (TCR) TCR α and TCR β chains

¹No diversity region in TCRa.

(Char *et al.*, personal communication). This may suggest repertoire differences in the TCR2 and TCR3 populations.

When TCR2 cells are suppressed by embryonic injection of anti-TCR2 monoclonal antibody and subsequent thymectomy, the treated chickens acquire increased levels of TCR3 cells but are deficient in TCR2 cells (Chen et al., 1989; Cihak et al., 1991). These TCR2-depleted birds appear healthy and they can respond normally to many T cell-dependent and T cell-independent antigens (unpublished data). Their serum IgG and IgM concentrations are also normal but their capacity for IgA production is severely compromised (Cihak et al., 1991). Secretory IgA concentrations in bile and lung lavage fluid are reduced 1,000- to 10,000-fold, and secretory IgA antibodies are not produced in response to mucosal immunization. These results indicate the importance of TCR2 cells in IgA production.

TCRβ Genes

Definition of the chicken TCR α and TCR β genes has provided insight into the molecular basis for the differences in the two $\alpha\beta$ T cell subsets. The cloning of the TCR β chain was achieved by cross-hybridization of a chicken cDNA library with fragments of a mixture of mammalian

TCR^β DNA under low stringency conditions (Tjoelker *et al.*, 1990). A chicken TCR β cDNA encodes a protein of approximately 300 amino acids including leader (L), variable (V), joining (J), diversity (D), and constant (C) regions (Figure 1). Although chicken and mammalian TCR β chains display only approximately 30% overall amino acid sequence identity, a number of conserved structural features are observed. These include consensus amino acids that are found in the most mammalian TCRB chains, the cysteine residues that form intra- and interdisulfide bonds, and a positively charged lysine that is thought to form a salt bridge with a negatively charged amino acid of CD3 molecules in the transmembrane domain (Bernot and Auffray, 1991).

The TCR β locus contains mammaliantype, V, D, J, and C segments (Tjoelker *et al.*, 1990; Cooper *et al.*, 1991). The exon structure of the C region is virtually identical with that of mammals. The genomic V, D, and J elements are flanked by classical heptamernonamer recombination signal sequences. As in mammals, the TCR β repertoire in the chicken is created by ordered recombination of V-D-J segments. However, the chicken TCR β locus is much simpler in that it contains only two V β families and does not feature a duplication of the J and C regions (Tjoelker *et al.*, 1990; Lahti *et al.*,



FIGURE 1. Sketch depicts overall T cell receptor (TCR) $TCR\alpha\beta$ structure and indicates disulfide bonds, possible N-glycosylation sites (CHO), leader (L), variable (V), diversity (D), joining (J), and constant (C) regions. The consensus amino acid residues and their positions are listed by protein structure.

1991). Within each V β gene family, most chicken strains contain approximately 6 members of the V β 1 and 3 to 5 members of the V β 2 family, although 17 V β 1 members have been identified in the chicken strain H.B19 (Dunon *et al.*, 1994). Likewise, only four relatively similar J segments are identified. Thus there is a limited capacity for combinatorial diversity in the avian TCR β repertoire. Instead, the CDR3 sequences formed by VD and DJ recombination with N-sequence additions are unique for each TCR β (McCormack *et al.*, 1991).

TCRα Genes

The chicken TCR α genes have only recently been identified. The TCRa proteins were isolated by antibody affinity chromatography and peptide sequences were determined. Degenerate oligonucleotide probes were then used to identify $TCR\alpha$ cDNA. A TCR α cDNA clone consists of 1.7 kb containing a 375-bp 5' untranslated region, a 503-bp 3' untranslated region, and an open reading frame of 825 bp (Göbel et al., 1993). The predicted 275 amino acid TCR α chain contains V, J, and C regions. Although chicken TCR α shares only 26% overall homology with its mammalian counterpart, most of the consensus amino acids thought to be important for structural integrity of the mammalian TCR α chains are conserved (Figure 1). Genomic analysis reveals multiple J segments and at least one V α family that contains approximately 25 members. The classical heptamer and nonamer recombination signal sequences and length of the spacer between them are conserved. In contrast to the mammalian and avian TCR β loci, however, a single exon encodes the avian L α and V α . A comparison of TCR α and β chains is shown in Table 3.

TCR2 and TCR3 Cells Use Distinct V_β Families. The relationship between TCR gene usage and the TCR2 and TCR3 sublineages defined by mAb was analyzed by Northern blotting. Both TCR2 and TCR3 cells contain C α and C β mRNA, confirming that they are subsets of $\alpha\beta$ T cells. Although the same $D\beta$ and $J\beta$ are shared by both subsets, the TCR2 cells contain only V β 1 transcripts and TCR3 cells contain only V β 2 mRNA (Lahti et al., 1991). Furthermore, TCR2 cells undergo V-D-J joining by deletional rearrangement, whereas TCR3 cells undergo V-D-J joining by inversional rearrangement (Table 2). This might explain why the V β 1 gene segment rearranges prior to $V\beta 2$ segment during ontogeny. Interestingly, mammalian TCR β chain sequences can be subdivided into two subgroups, V β I and V β II, based on the structural similarities of the proteins (Schiffer et al., 1992), and these same structural features are conserved in chicken V β 1 and V β 2 (Tjoelker *et* al., 1990).

Characteristic	TCR2	TCR3
Appearance during ontogeny		
Thymus	E14 ²	E17
Spleen	E19	D2
Phenotype		
CD4:ĆD8 ratio	2:1 to 3:1	4:1
Tissue homing pattern		
Spleen	Periarteriolar sheaths	Periarteriolar sheaths
Intestine	Lamina propria	Rarely identified
Function	•••	
Helper activity for IgA production	Yes	No
Graft vs host	Quantitative differences de- pending on MHC pairing	Quantitative differences de- pending on MHC pairing
TCR β^2 usage	Vβ1 (1.1 to 1.17)	Vβ2 (2.1 to 2.5)
Mechanism of $V\beta$ rearrangement	Deletion	Inversion

TABLE 3. Two distinct $\alpha\beta$ T cell subpopulations in the chicken¹

 $^{1}TCR = T$ cell receptor.

²Embryonic day 14.

The V α usage by TCR2 and TCR3 cells may also contribute to their differences in function. To examine the utilization of $V\alpha$ segments by TCR2 and TCR3 cells, a panel of the defined cell lines was examined by Northern blot analysis. Under very stringent conditions 2 of 10 cell lines reacted with the V α 1 probe cloned from TCR2 cell line UG9 (Göbel *et al.*, 1993). Analysis of V $\alpha^$ cDNA clones has revealed multiple $V\alpha$ families in the chicken. Homology between the V α 1 and V α 2 members is only around 24%. Interestingly, both TCR2 and TCR3 cells can use $V\alpha^2$ family members, suggesting that V β 1 and V β 2 genes themselves govern functional differences in TCR2 and TCR3 T cells.

CONCLUDING REMARKS

Comparative studies reveal striking conservation of T cell development in avian and mammalian species. The relatively high frequency of $\gamma\delta$ T cells in the chicken and the experimental accessibility of the embryo make birds a valuable model for study of the early divergence in the $\alpha\beta$ and $\gamma\delta$ T cell lineages as well as the physiological role of $\gamma \delta$ T cells. The two subsets of $\alpha\beta$ T cells recognized by TCR2 and TCR3 mAb express prototypic VBI and V β II genes, and they differ in their ontogeny, tissue distribution, and function. It is not yet known whether or not the two $\alpha\beta$ subpopulations utilize different V α genes. The relative simplicity of the avian $\alpha\beta$ TCR gene loci may thus reveal basic principles in T cell physiology that are difficult to appreciate in more complex mammalian systems. Finally, our studies in the chicken model suggest that $\gamma\delta$ and $\alpha\beta$ T cells are functionally interdependent.

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