マウス異種抗リンパ球抗体のマウスリンパ球に対する交差反応

誌名	Japanese journal of veterinary science
ISSN	00215295
著者	山本, 博
巻/号	47巻3号
掲載ページ	p. 371-378
発行年月	1985年6月

Cross-reactivities of Mouse Anti-Xenogeneic Lymphocyte Antisera with Mouse Lymphocytes

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(Received 17 December 1984/Accepted 8 February 1985)

ABSTRACT. Cross-reactive antibodies which were reactive with mouse lymphocytes were detected in mouse antisera raised against lympocyte of the dog, chicken, bull frog or fish (*Carassius carassius*). All of the four xenoantisera crossreacted with the lymphocytes of A.TL(I^k), B10.BR(I^k), B10.A(I^a), B10.S(9R)(I^{t4}) and B10.D2(I^a), but not with those of A.TH(I^s) and B10.S(I^s). The xenoantisera raised against dog lymphocytes crossreacted with C57BL/6(I^b) lymphocytes, but the other three xenoantisera did not. Genetic mapping studies of the cross-reactive antibodies in the mouse indicated that the crossreaction of the four xenoantisera was attributable to antibodies to the Ia molecule similar to the *I-E* subregion gene product. In the case of A.TH anti-dog xenoantisera, antibodies to the Ia molecule similar to the *I-A* subregion gene product were also found. The cells cross-reactive with these four xenoantisera and Ig-positive B lymphocytes were enriched in the nylon-wool adherent fraction of B10.BR spleen cells, and depleted in the nylon-wool non-adherent fraction. These results showed that the xenoantisera crossreacted with the Ia antigens which are predominantly expressed on the surface of Ig^+B lympocytes. These results confirmed the specificity of the crossreactions detected by A.TH(I^S) anti-A.TL(I^k) alloantiserum, and further indicated that the crossreactive genes are the homologues of the mouse *I-E* subregion gene in the chicken, frog and fish, and of the *I-A* and *I-E* subregion genes in the dog.—KEY WORDS: Ia antigen, interspecies crossreaction, xenoantiserum.

Jpn. J. Vet. Sci. 47(3): 371–378, 1985

Genes within the major histocompatibility complex (MHC) are distinguished by their allelic polymorphism. It is generally believed that such polymorphism itself is relevant to their natural functions. Recent advances in cellular immunology and immunogenetics have shown that the porducts of the MHC genes play crucial roles when T lymphocytes interact with other cells and recognize antigens displayed on the cell surface [12, 14, 15, 21]. T cells can effectively recognize antigens only in the context of the MHC gene products. Nevertheless, the precise function of MHC and the biological significance of such functional restrictions imposed on T cell recognition are yet to be studied. Studies of the phylogenetic relationships among these genes may also provide an insight into the function and structure of these gene products by revealing their evolutionary behavior.

The *I* region of the mouse *H-2* complex has been subdivided into five subregions (A, B, J, E, C) on the basis of serological and functional analyses of intra-MHC recombinant strains [7]. However, no serologically detectable specificities nor Ir genes have been localized to the *I-E* subregion of the $H\text{-}2^b$ and $H\text{-}2^s$ haplotypes. Attempts to identify *I-E* gene products of these haplotypes by chemical analysis have so far been unsuccessful [4, 6, 10]. Thus, the *H-2* complex of these haplotypes seems not to express *I-E* subregion genes. In this case, alloantisera raised in "*I-E* negative" strains of mice against "*I-E* positive" mouse cells might contain, in

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Table 1. Mouse strains and their H-2 haplotypes

Strains	H-2 haplotype	H-2 regions							
		K	I-A	I-B	I-J	I-E	I-C	S	D
A.TH	t2	s	s	s	s	s	s	s	d
A.TL	t1	s	k	k	k	k	k	k	d
B10.S	s	s	s	s	s	s	s	s	s
B10.BR	k	k	k	k	k	k	k	k	k
B10.A	a	k	k	k	k	k	d	d	d
B10.S (9R)	t4	s	s	?	k	k	d	d	d
C57BL/6	b	b	b	b	b	b	b	b	b
B10.D2	d	d	d	d	d	d	d	d	d

addition to the usual alloantibodies, the antibodies reactive with conserved portions of *I-E* molecules inherited from a hypothetical primordial gene (*I-Eo*) which might have existed long before the speciation of contemporary animals. Such antibodies would show extensive cross-reactions with the *I-E* homologues of various species of animals. Interspecies cross-reactions of anti-Ia mouse alloantibodies have indeed been observed. Although such a cross-reaction was first found between mouse *I-A* and rat Ia homologues, subsequent studies indicated much broader and more frequent interspecies cross-reactions of anti-*I-E* antibodies [8, 9, 13, 16, 18].

Mouse alloantisera raised against Ia antigens (class II major histocompatibility antigens) frequently show cross-reactions with the Ia homologues of other species [8, 9, 13, 16, 17, 18]. Especially, such cross-reactions could be readily detected with the antisera containing antibodies to Ia. 7, a serological determinant present on the *I-E* molecules. In another report, we showed the results of a systematic examination of the interspecies cross-reactions of murine anti-Ia alloantibodies on a variety of vertebrate species [20]. The results indicated that the cross-reactions extended not only to all mammalian species studied but also to submammalian vertebrates.

In order to confirm these observations, antisera raised in the reverse directions, i.e., mouse antisera raised against lymphocytes of the dog, chicken, bullfrog or fish were tested for their reactivities with lymphocytes of *H-2* congenic strains of mice and genetic specificities of these cross-reactions were determined.

MATERIALS AND METHODS

Animals: Adult mice of the following strains were used; A. TH($H\text{-}2^s$), A. TL ($H\text{-}2^{t1}$), C57BL/6($H\text{-}2^b$), B10.A ($H\text{-}2^a$), B10.BR ($H\text{-}2^k$), B10.D2($H\text{-}2^d$), B10.S ($H\text{-}2^s$), and B10.S(9R) ($H\text{-}2^{t4}$). These mice were bred in our own animal facilities. The haplotypes of these mice are shown in Table 1. Dogs and chickens were obtained from local breeders. The fish (*Carassius carassius*) were purchased from a local pet shop. Frogs (*Rana catesbeiana*) were purchased from Nippon Seibutsu Zairyo Center (Tokyo).

Preparation of cells: Mouse spleen lymphocytes were obtained by gently disrupting spleens by forceps after perfusion with Hank's balanced salt solution. Red cells were lysed by resuspending the cells in NH_4Cl_2 solution supplemented with Tris buffer pH 7.5. Peripheral blood lymphocytes (PBL) and spleen lymphocytes other than those of mice were separated from red cells by centrifugation on Ficoll-Conray solution. Separation of lymphocytes by a nylon-wool column was performed by the method of Julius *et al.* with a minor modification [3, 5].

Antisera: Mouse A. TH anti-A. TL alloantiserum (Serum #201) was obtained by im-

munizing A. TH mice with A. TL skin grafts followed by biweekly i.p. injections of 2×10^7 live spleen cells beginning at the third week after the skin graft. The xenogeneic antisera were prepared by immunizing mice with lymphocytes of various species of animals in the following combinations; A. TH anti-dog PBL, A. TH anti-chicken PBL, A. TH anti-frog spleen cells, and A. TH anti-fish spleen cells. These recipients were injected i.p. with $1–2\times10^7$ cells per immunization. After four injections, bleeding was started and antisera of each combination were pooled. Pooled sera were decomplemented (56°C, 30 min.).

Cytotoxicity assay: Two stage trypan blue cytotoxicity tests were performed in U bottomed-microtiter plates using prescreened rabbit complement as described by Sachs *et al.* [13]. Briefly, 10 μl of cell suspension (5×10^6/m*l*) and 10 μl of serially diluted serum were mixed and incubated for 15 min at 37°C. Cells were washed once and incubated with appropriately diluted rabbit complement for 30 min at 37°C. Plates were centrifuged and viability of cells was determined microscopically by their trypan blue uptake.

Absorption: In vitro absorption test of xenoantiserum was performed by the following procedure. 1.5×10^8 packed absorbing cells were mixed with 500 μl of the antiserum diluted to 1:10. The mixture was incubated on ice for 30 min and then centrifuged to remove the cells. This procedure was repeated twice. In each instance, the absorbed serum was tested for cytotoxicity to the cells from the absorbing strain to establish that all the reactive antibodies had been successfully removed.

Surface immunoglobulin: The number of Ig-positive (Ig^+) cells in each population fractioned by nylon-wool column was calculated by immunofluorescence critertion as described by Dickler and Sachs [2], using a fluoresceinated rabbit anti-mouse immunoglobulin (RAMIG) antibody (Cappel Laboratories, U.S.A.). Briefly, equal amount of lymphocytes (20×10^6/m*l*) suspended in 2% bovine serum albumin in phosphate-buffered saline, 0.02% Na Azide (BSA-PBS) pH 7.2 and RAMIG (0.5 mg/m*l* in PBS pH 7.2) were mixed and incubated 30 min at 4°C. The cells were then washed three times with BSA-PBS pH 7.2, and wet amounts were prepared in the same medium. The cells on the slides were read using ultraviolet light as described by Dickler [1]. Not less than 100 small lymphocytes per preparation were evaluated.

RESULTS

Cross-reactions of mouse anti-xenogeneic lymphocyte antisera on mouse lymphocytes: As depicted in Fig. 1, all of the four antisera raised in A. TH (I^s) reacted with A. TL (I^k) spleen cells, and not with A. TH and B10.S spleen cells. Since spleen cells of A. TH (I^s) reacted with none of the antisera and A. TL (I^k) spleen cels reacted with all of them, and these two strains are only different in their intra-*H-2* regions, the cytotoxicity of these antisera was shown not to be due to the antisera raised against extra H-2 region gene products. As shown in Table 2, all of the four antisera raised in A. TH (I^s) mice against both mammalian and non-mammalian lymphocytes also showed cross-reactions on B10.BR (I^k), B10.A (I^a), B10.S (9R) (I^{t4}) and B10.D2 (I^d) spleen cells. In addition, in the case of antisera raised against dog lymphocytes, cross-reactions were also observed with C57BL/6 (I^b) spleen cells.

Genetic specificities of mouse anti-xenogeneic lymphocyte antisera: Reactivity of the four mouse xenoantisera on A. TL (I^k) and B10.S (9R) (I^{t4}) spleen cells located the gene encoding the cross-reactive antigen between the *I-B* and the *D* regions of the *H-2* complex (Table 3). Only the *I-E* subregion is known to encode the classical Ia antigens within this chromosomal segment. Thus, these results indicated that the cross-reaction of the four

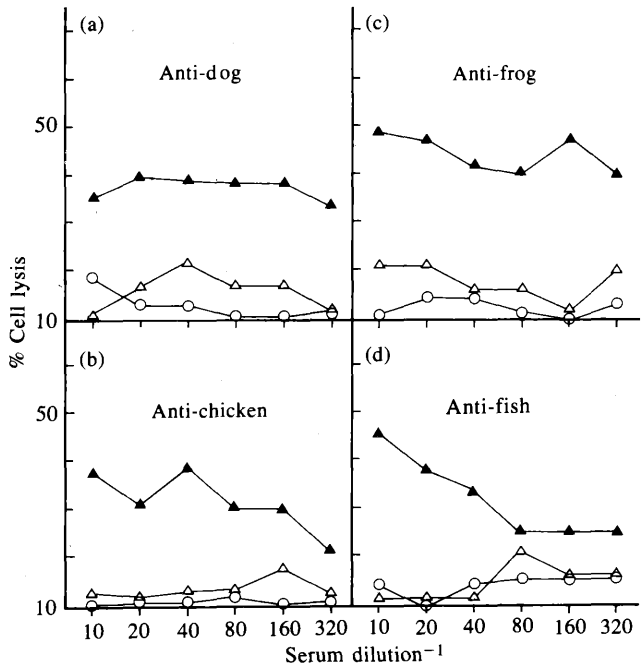

Fig. 1. Cross-reactions of mouse anti-xenogeneic lymphocyte antisera with spleen cells of H-2 congenic mice. Reactivities of the antisera were examined by cytotoxicity assay for spleen cells of the following H-2 cengenic strains; A. TH ○ , A. TL ▲ , B10.S △

Table 2. Cross-reactions of mouse anti-xenogeneic lymphocyte antisera with mouse lymphocytes

Antisera[a)]	% Dead cells from mouse spleen							
	B10.BR	A.TH	B10.S	A.TL	B10.A	B10.S (9R)	B6	B10.D2
C alone	18	14	15	10	18	14	12	16
B10.S anti-Dog	65	15	14	39	66	42	39	61
A.TH anti-Chicken	44	11	11	32	48	35	10	ND
A.TH anti-Frog	45	17	19	37	47	36	19	ND
A.TH anti-Fish	31	12	13	37	47	41	13	ND

a) 10 times dilution of mouse antisera was used.

xenoantisera was attributable to the antibodies to the Ia molecule of the *I-E* subregion gene products.

In the case of the mouse xenoantisera to the dog, the genetic specificities of the cross-reactions on $H\text{-}2^b$ lymphocytes have been examined by absorption test with B10.S (9R) (I^{t4}) spleen cells. Table 4 shows that the xenoantisera raised against dog lymphocyte cross-reacted with C57BL/6 (I^b) spleen cells, while the xenoantisera that were absorbed with B10.S (9R) (I^{t4}) spleen cells did not cross-react any more. Since only the *I-A* subregion is known to encode the classical Ia antigens between the *K* and *I-J* subregions, these results showed that the cross-reaction of the xenoantisera raised against dog lymphocytes with C57BL/6 (I^b) spleen cells was attributable to the *I-A* homologues subregion gene.

Table 3. Cross-reactions of mouse xenoantisera raised against mammalian and submammalian lymphocytes with allogeneic mouse spleen cells

Target spleen cells	H-2 subregion								Reactivity with spleen cells in the presence of			
	K	A	B	J	E	C	S	D	A.TH anti-dog	A.TH anti-chicken	A.TH anti-frog	A.TH anti-fish
A.TH	s	s	s	s	s	s	s	d	−[a]	−	−	−
A.TL	s	⌈k→	k	k	k	k	←k⌋	d	+[b]	+	+	+
B10.S	s	s	s	s	s	s	s	s	−	−	−	−
B10.S (9R)	s	d	?	⌈k→	k	d	←d⌋	d	+	+	+	+

a) <10% above complement background.
b) >25% above complement background.

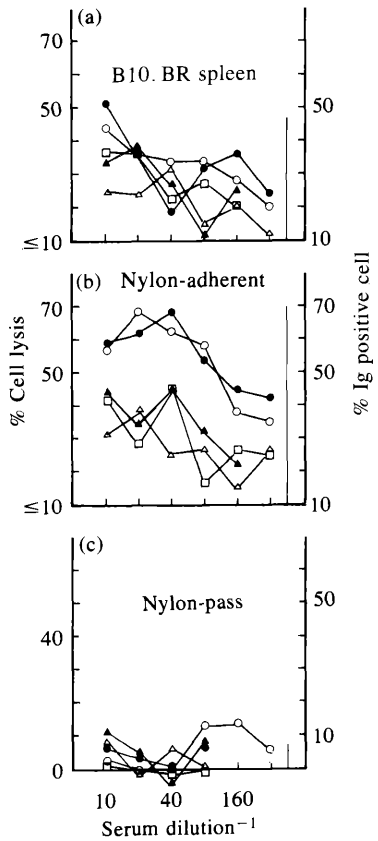

Fig. 2. Cytotoxicity of mouse xenoantisera raised against mammalian and submammalian lymphocytes, and immunofluorescent staining by fluoresceinated rabbit anti-mouse immunoglobulin antibody of nylon-wool fractionated B10.BR spleen cells. Cytotoxicity of Serum #201 (A. TH anti A. TL) (●—●), of mouse xenoantisera raised against dog (○—○), chicken (□—□), frog (▲—▲) and fish (△—△).

The cell populations of mouse cross-reactive with xenoantisera: To determine the cell populations of mouse that were cross-reactive with these xenoantisera, B10.BR (I^k) spleen cells were fractioned by nylon-wool column and each fraction of cells was examined by both cytotoxic test and immunofluorescent antibody technique (Fig. 2). Fig. 2a shows that about 50% of B10.BR spleen cells was cross-reactive with Serum #201 and 45% was cross-reactive with mouse xenoantisera to the dog, but smaller percentages were cross-reactive with the other three xenoantisera. The percentage of Ig^+ cells present in the whole B10.BR spleen cells was 45%. Therefore, in the case of Serum #201 and mouse xenoantisera to the dog, the percentages of the cytotoxicity and Ig^+ cells were almost same, but the other three xenoantisera were not so cross-reactive with B10.BR spleen cells. Fig. 2b shows the cross-reactions of Serum #201 and the four mouse xenoantisera, and the percentage of Ig^+ cells in nylon-wool adherent fraction of B10.BR spleen cells. The percentages of the cross-reactions of Serum #201 and the xenoantisera to the dog were both about 70% and those of the other three xenoantisera were about 30–45%. In this fraction, the percentages of Ig^+ cells were 70%. Fig. 2c shows that the percentages of the cells containing the cross-reactive antigens and Ig on their surface were

5–10% in the B10.BR spleen cells that passed through the nylon-wool column. These results showed that the cells cross-reactive with these four xenoantisera and Ig^+ B cells were enriched in the nylon adherent fraction of B10.BR spleen cells, and depleted in the nylon non-adherent fraction.

DISCUSSION

Interspecies cross-reactions of anti-Ia alloantibodies was first found between the *I-A*^{k} antigen of the mouse and the Ia-like antigen of the rat [13]. Subsequent studies on human [8] and pig [16] lymphocytes revealed that such interspecies cross-reactions were also detectable with mouse alloantibodies to the *I-E* antigens. It has been shown that certain anti-Ia antibodies present in an A. TH anti-A. TL mouse alloantiserum show extensive interspecies cross-reactions with a wide variety of vertebrate species including non-mammalian as well as mammalian species [20]. In all cases, the specificity of the cross-reactive antibodies were shown to be directed to the products of the *I-E* subregion gene by absorption studies using lymphocytes of *H-2* congenic and recombinant strains of mice. In order to confirm these observations, studies on cross-reactions of mouse antisera raised against xenogeneic cells on *H-2* congenic mouse lymphocytes were carried out. In the present experiments (Table 2, Table 3), all of the four antisera were shown to contain antibodies cross-reactive with the mouse *I-E* gene products. In the case of the antisera raised against dog lymphocytes, the present study showed other cross-reactions on *I*^{b} lymphocytes (Table 2). From the absorption study using the B10.S (9R) (*I*^{14}) spleen cells, it was shown that these cross-reactions between mouse xenoantisera raised against dog lymphocytes and C57BL/6 (*I*^{b}) spleen cells are attributable to the mouse *I-A* homologues subregion genes (Table 4). In several mammalian species including dog, recent reports have also shown the existence of anti-Ia monoclonal alloantibodies reactive with both *I-A* and *I-E* molecules [11, 19].

Table 4. Cross-reactions of mouse xenoantisera

Target spleen cells	H-2 subregion							
	K	A	B	J	E	C	S	D
B10.S (9R)	s	s	?	k[a)]	k	d	d	d
C57BL/6	b	b	b	b	b	b	b	b

a) After absorption of the mouse xenoantisera with ducts persisted.

The results of cytotoxicity and immunofluorescence on B10.BR (*I*^{k}) spleen cells fractionated by nylon-wool column tested with mouse xenoantisera (Fig. 2) show that the cross-reactive antigens are predominantly expressed on te surface of Ig^+ B lymphocytes. Cross-reactions of mouse anti-dog xenoantisera showed almost the same antibody titer (Fig. 2b), as A. TH anti-A. TL alloantiserum, but the xenoantisera raised against chicken, frog and fish lymphocytes did not. This is probably because the xenoantisera raised against dog lymphocytes contains the antibodies reactive with *I-A* and *I-E* homologues, whereas the xenoantisera raised against chicken, frog and fish lymphocytes contain only the antibodies reactive with only the *I-E* gene products.

Thus, from the genetic specificity and the population of cells bearing these cross-reactive antigens, the cross-reactive antibodies found in these xeno-specific antisera appeared to be directed to the *I-E* antigen in the mouse. These results confirmed the specificity of the cross-reactions detected by A. TH (*I*^{s}) anti-A. TL (*I*^{k}) alloantiserum. Furthermore, the cross-reaction of the A. TH (*I*^{s}) anti-fish antiserum with *H-2*^{k} lymphocytes indicated that anti-Ia cross-reaction extends even to bony fish. Therefore, the cross-reactive antigens detected on the surface of dog,

raised against mammalian and submammalian lymphocytes with allogeneic mouse spleen cells

% Dead cells in the presence of								
C alone	A.TH α-Dog	A.TH α-Dog B10.S (9R)	A.TH α-Chicken	A.TH α-Chicken B10.S (9R)	A.TH α-Frog	A.TH α-Frog B10.S (9R)	A.TH α-Fish	A.TH α-Fish B10.S (9R)
14	42	14	35	12	30	14	41	14
11	39	33	10	12	19	12	13	17

B10.S (9R) spleen cells, the cross-reactive antibodies raised against I-A or I-B subregion gene pro-

chicken, frog and fish cells probably represent products of genes homologous to murine *I* region genes.

Ia antigens have been shown to play an essential functional role in the complex interaction network of the immune system [12, 16, 19]. T lymphocytes have to recognize self Ia antigens as well as nominal antigens in order to be effectively stimulated by the antigens. However the molecular mechanism and biological significance of such restricted recognition of antigens by T cells are not known. Characterization of molecular features of putative *I-E* homologues in primitive animals, and studies on the functions of these molecules and Ia positive cells in the primitive immune systems may provide a clue to understand the evolutionary significance of the structure and function of these gene products. The interspecies cross-reactive anti-Ia antibodies described in this communication could provide a powerful tool as a general probe to study evolutionary aspects of these gene products.

ACKNOWLEDGEMENTS. The author wishes to thank Drs. Masaru Taniguchi and Nobukata Shinohara, Department for Immunology Chiba University, School of Medicine, for their encouragement and helpful supports to this work.

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要　約

マウス異種抗リンパ球抗体のマウスリンパ球に対する交差反応: 山本　博(千葉大学医学部付属免疫研究施設)——マウス *I-E* 亜領域の遺伝子にコードされ，広く他種動物の Ia 抗原と交差することが知られる Ia 抗原 *Ia·7* が欠落する A·TH(I^s) マウスを，イヌ・ニワトリ・ウシガエル・フナのリンパ球で免疫して得た抗血清について，マウスリンパ球に対する交差反応性を調べた。4種の異種リンパ球に対する抗血清は主としてマウスB細胞と反応し，A·TH(^{s}) および B10·S(I^s) マウスリンパ球とは反応せず，A·TL(I^k)，B10·BR(I^k)，B10·A(I^a)，B10·S(9R) (I^{t4})，および B10·D2(I^d) マウスのリンパ球 Ia 抗原，すなわち *I-E* 亜領域ハプロタイプ *K* または *d* のマウスリンパ球の Ia·7 と反応した。また，抗イヌリンパ球血清は C57BL/6(I^b) マウスリンパ球とも反応し，B10·S(9R) (I^{t4}) マウスリンパ球で吸収すると，*I-A* 亜領腎由来 Ia 抗原と反応した。以上の成績から，マウス同種抗 Ia(*I-E*) 抗体と交差反応を示す抗原がイヌ・ニワトリ・カエル・フナのリンパ球に存在することが，イヌのリンパ球 Ia とマウスの I-A 亜領域由来 Ia との間には共通抗原が存在することが示唆された。