Some Properties of Cross Reacting Antibody of the ABO Blood Group System

By A. Richardson Jones and Lorraine Kanef

In a previous communication we have described applications of the mixed agglutination reaction to studies of the behavior of low-concentration minor cell components of mixed populations of erythrocytes. This reaction is well suited to investigation of the behavior of isoagglutinins of the ABO group system since antigen-antibody reactions within this group system may be readily detected when the antigenically specific cell is diluted in "inert" cells to concentrations of the order of 1 part in 500 or less. At this concentration reactions between an isoagglutinin and a specific minor population erythrocyte may be carried out without giving rise to agglutination of the sensitized cell.

One of the problems chosen for study by the mixed agglutination technic was the definition of the so-called "cross reacting antibody" which is found in the serum of certain group O individuals. This antibody was originally detected by Moss through the observation that absorption of a group O serum with group A cells removed not only a proportion of the anti-A isoagglutinin but also some of the anti-B activity of the serum. It was further shown that absorption of a group O serum with group B cells resulted in a reduction of its anti-A titer as well as the expected reduction of anti-B titer.

Demonstration of the power of some group O serums to cross react with group A and B cells was also made by Koeckert, who showed that some anti-B activity was present in eluates made from group A cells which had been exposed to group O serum and, also, that anti-A activity could be found in eluates from group B cells treated with group O serum.

The clinical importance of cross reacting antibody has been clearly demonstrated by Rosenfield, who found it to be consistently present in the serum of group O mothers whose infants suffered from erythroblastosis due to ABO incompatibility.

Attempts to provide an adequate theoretical explanation of the cross reacting property of group O serum has led to the establishment of two schools of thought. These are summarized as follows: (1) That there exists in certain group O serums an antibody molecule with the combined specificity "anti-A + B." This molecule is visualized as being bivalent in the special sense of possessing two differing specificities. (2) That the cross reacting activity of group O serum is due to the presence of a third isoagglutinin, additional to anti-A and anti-B, named anti-C by Moss. It is postulated that group A, group

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B and group AB cells possess the corresponding antigen C, whereas group O cells lack this antigen.

The purpose of the present study was to test, by experiment, the validity of each of these conflicting hypotheses.

The principal experimental technic used in this investigation was an application of the mixed agglutination reaction to the detection of cross reacting antibody in group O serums. This technic has been described in detail elsewhere, but the principles of the method will be outlined again in this communication.

**PRINCIPLES OF DETECTION OF CROSS REACTING ANTIBODY**

A mixture of washed group O and group A erythrocytes is prepared such that the relative concentration of group A to group O cells is 1:500. The group A cells are thoroughly dispersed among the group O cells, and the mixture is exposed to the action of serum from a group O donor for approximately 15 minutes at 20 C. with frequent mixing. At the end of this time all free isoagglutinin is removed by 4 washes in isotonic saline. The group A cells in this suspension may now be considered to be sensitized by both the anti-A and the cross reacting antibody (if this was present) in the serum. The sensitized cells will not have been agglutinated by this procedure because of their extreme dispersion among the nonreactive group O cells. If it is assumed that the antibody which has sensitized the group A minor population cells is bivalent, the introduction of an additional supply of group A cells into the suspension will provide a means for this antibody to complete a lattice. It can be readily demonstrated that this, in fact, takes place. The addition of cells capable of combining with the exposed ends of the antibody molecules present on the minor population cells results in the formation of characteristic spherical agglutinates which have been shown to consist of a central minor population cell surrounded by a shell of added cells. The appearance of these agglutinates is illustrated in figure 1. In previous communications we have referred to the added cells as "detector cells" and have shown that this reaction is immunologically specific. When cross reacting antibody is present in the sensitizing serum, it is found to confer on the sensitized group A minor population cells the property of producing characteristic mixed agglutinates on the addition of group B detector cells.

The general form of this experiment can be repeated with the substitution of group B cells as the minor population. The presence of cross reacting antibody will now be revealed by the ability of the sensitized group B minor population cells to form mixed agglutinates with group A detector cells. In these experiments the specificity of the lattice formation is controlled by adding group O detector cells to an aliquot of the sensitized washed population mixture.

**EXPERIMENT 1**

The purpose of this experiment was to determine the spatial relationship between the site of action of the cross reacting antibody in group O serum and the antigens A or B of the cell. In order to do this a population mixture consisting of 1 part of group A1 cells and 500 parts of group O cells was exposed to the action of anti-A serum from a group B donor. The object of this procedure was to block the A antigen sites with anti-A. If cross reacting antibody combined with the red cell at a site other than the A antigen site, it would be expected that blocking the A antigen would have no influence on the ability of the cell to combine with cross reacting antibody. On the other hand, if a blocked cell failed to react with cross reacting antibody it
would be necessary to infer that the combining sites for both anti-A and cross reacting antibody were effectively identical. This experiment was carried out with the use of both group A minor population cells blocked with anti-A and with group B minor population cells blocked with anti-B.

**Material and Methods**

Population mixtures were prepared by diluting .05 ml. of 5 per cent suspensions of group A and group B washed cells each to 25 ml. with a 5 per cent suspension of washed group O cells. This yielded two suspensions in which the relative concentrations of group A and group B cells to the group O cells was of the order of 1:500. It was found convenient to identify each of these suspensions as O(A) and O(B), respectively.

All serums used in these investigations were treated to suppress any tendency which they might have to cause anomalous mixed agglutination by dissolving in them the tetrasodium salt of EDTA to a concentration of approximately 1 mg./ml. In carrying out titrations of the treated serum 2-fold serial dilutions were made with the use of buffered isotonic saline as diluent to which sodium EDTA had been added to a concentration of 10 mg./100 ml. Dilutions were carried to the tenth power.

A 3 ml. aliquot of the O(A) suspension was mixed with an equal volume of anti-A serum. Another aliquot of the same suspension was mixed with serum from a group AB donor (i.e., an “inert” serum). Similar aliquots from the O(B) suspension were mixed with equal volumes of anti-B serum, and with “inert” serum, respectively. All 4 tubes were incubated for 15 minutes at 20 C. with frequent mixing. At the end of the incubation period all suspensions were washed 4 times in isotonic saline.

A set of 2-fold serial dilutions was then prepared from a group O serum which was known to contain cross reacting antibody. Each dilution was divided into 4 aliquots, and
to each aliquot was added 1 of the 4 previously prepared suspensions. By this means
the same group O serum was titrated against both "blocked" and "nonblocked" sus-
pensions of both O(B) and O(A) population mixtures. The contents of each tube in
this set of titrations were thoroughly mixed and incubated for 15 minutes at 20 C. At
the end of this time the suspensions in all tubes were washed 4 times in isotonic saline,
and then each was divided into 3 equal aliquots. To the first aliquot was added an
equal volume of a 5 per cent suspension group A detector cells, to the second aliquot was
added an equal volume of a 5 per cent suspension of group B detector cells and to the
third aliquot was added an equal volume of a 5 per cent suspension of group O cells. The
contents of all the tubes were mixed by shaking and were then gently centrifuged. After
centrifugation the tubes were shaken with just sufficient force to redisperse the "button"
of cells and centrifuged and gently shaken a further 2 times. The suspensions in each
tube were then examined in a hemocytometer chamber under the microscope. A positive
result was scored if characteristic mixed agglutinates were observed in the suspension. A
negative result was scored if the agglutinates were absent.

Results

Table 1 summarizes the results of the experiment. It will be seen that
the titration of the serum containing cross reacting antibody against both
O(A) and O(B) population mixtures in the "nonblocked" form yielded
substantially similar results. There is ample evidence that the binding of a
group A minor population cell to a group B detector cell and the binding
of a group B minor population cell to a group A detector cell has occurred.
The specificity of these reactions is proved by the complete absence of
agglutination in those tubes to which group O cells had been added in lieu
of detectors. The direct binding of the group A minor population cell to the
group A detector cell and the group B minor population cell to the group
B detector cell occurs independently of the dilution of group O serum to
which the population mixture was exposed. This is because the antibody
used for blocking the minor population cell in these cases is itself capable
of forming a lattice.

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<tr>
<th>Detectors</th>
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*+ indicates the presence of mixed agglutinates.
0 indicates the absence of mixed agglutinates.
Inspection of the results of that section of the titration involving the "blocked" cells shows that the ability of these cells to accept cross reacting antibody from the group O serum is severely limited. The blocked O(A) and the blocked O(B) suspensions appear to be virtually incapable of combining with group B or group A detector cells, respectively.

**Experiment 2**

In this experiment a number of serums were titrated against O(A) and O(B) population mixtures with the object of determining the titer of cross reacting antibody. These serums were tested as part of a study designed to establish the relationship between the titer of cross reacting antibody in the serum of group O pregnant women and the subsequent development of erythroblastosis in their newborn infants. The findings of this study will be reported in detail elsewhere, but certain of the results are cited here because they are considered relevant to the definition of the properties of cross reacting antibody.

**Material and Methods**

O(A) and O(B) population mixtures were prepared as described in the foregoing section.

The serum under investigation, treated with EDTA, was serially diluted in EDTA-saline. Each dilution was divided into 2 equal parts in order to produce 2 identical sets of dilutions. To all tubes of one set of dilutions was added unit volume of the O(A) population mixture and to all tubes in the second set was added unit volume of the O(B) population mixture. After shaking, the tubes were allowed to stand at room temperature for 15 minutes.

After this incubation period the cell suspensions in all tubes were washed 4 times in isotonic saline. The contents of each tube were then further subdivided into 3 aliquots. To the first aliquot was added an equal volume of a 5 per cent suspension of group A detector cells. To the second aliquot was added an equal volume of a 5 per cent suspension of group B detector cells and to the third aliquot was added an equal volume of group O cells. The cell suspensions in the tubes were thoroughly mixed by shaking and then all were subjected to the same gentle centrifugation and shaking procedure outlined in the previous section, prior to being examined under the microscope.

The results of the reactions were scored as positive or negative depending upon the presence or absence of characteristic mixed agglutinates.

**Results**

Although a large number of serums have been examined by this method, only the results of 3 typical titrations are given here as being illustrative of the 3 main categories into which the behavior of cross reacting antibody falls.

Table 2 summarizes the results of a cross reacting antibody titration in a case in which the antibody possesses the ability to bind a group A cell to a group B cell as strongly as it binds a group B to a group A cell. The cross reacting titer of the serum is the same for an O(A) population mixture as it is for an O(B) population mixture.

Table 3 shows the results obtained with another serum which possessed a cross reacting antibody which had the property of binding a group B
Table 2.—The Results of Titrating a Cross Reacting Antibody Which Links Group A and Group B Cells Symmetrically

<table>
<thead>
<tr>
<th>Dilutions of cross reacting serum</th>
<th>Detectors</th>
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<th>32</th>
<th>64</th>
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<tbody>
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<td>O(A) mixture</td>
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*+* indicates the presence of mixed agglutinates, 
0 indicates the absence of mixed agglutinates.

Table 3.—Titration Results of a Cross Reacting Antibody Which Links Groups A Cells to Group B Cells more Readily than it Links Group B Cells to Group A Cells

<table>
<thead>
<tr>
<th>Dilutions of cross reacting serum</th>
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*+* indicates the presence of mixed agglutinates, 
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detector cell to a group A minor population cell but which almost entirely lacked the ability to bind a group A detector cell to a group B minor population cell. This type of reaction will be referred to as an "asymmetric cross reaction." A third serum from this series has been used to illustrate a variety of asymmetric cross reaction which is the converse of the second serum. These results are given in table 4. It can be seen that the second variety of asymmetry is revealed by the cross reacting power of the serum being limited to its ability to bind only group B minor population cells to group A detector cells.

DISCUSSION

Although the existence of cross reacting antibody in group O serum was inferred by the earliest workers in the field, the evidence on which the inference was based was limited initially to the results of cross absorption experiments carried out by Moss,3 and later, reinforced by the results of the elution experiments of Koeckert.4 More recently Dodd7 carried the investigation of group O serums to a high degree of refinement by the use of an elution technic while Bird,8 by using a cross absorption method, appears to have been the first to call attention to the presence of asymmetric varieties of cross reacting antibody.

The application of mixed agglutination technics to the detection and measurement of cross reacting antibody has now made it possible to observe...
Table 4.—Titration Results of a Cross Reacting Antibody which Links Group B Cells
to Group A Cells More Readily than it Links Group A Cells to Group B Cells

<table>
<thead>
<tr>
<th>Dilutions of cross reacting serum</th>
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<td>B</td>
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<td>O</td>
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<td>O(B) mixture</td>
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<tr>
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<td>B</td>
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<td>O</td>
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* + indicates the presence of mixed agglutinates,
  o indicates the absence of mixed agglutinates.

directly the specific union of a group A cell to a group B cell through the medium of this antibody. One aspect of the mixed agglutination technic which is of peculiar advantage to the present study is the fact that it is possible to block either the A antigen site or the B antigen site without causing agglutination of the blocked cell. Although an attempt to define the location of Moss's hypothetical C antigen in relation to the A and B antigen sites was made by Koeckert, the value of his observations was limited by the fact that his attempts to block specific antigen sites in "pure" suspensions of cells were necessarily accompanied by agglutination of these cells. It was therefore not possible to exclude from an interpretation of his experiments the possibility that agglutination per se could have exerted a modifying influence on the blocking phenomenon. Furthermore, Koeckert does not make it clear that the serums used in all his experiments have been proved to contain cross reacting antibody. The results presented in table 1 show that the prior attachment of specific agglutinin to a group A or group B cell almost entirely eliminates its ability to accept a cross reacting antibody. Since the blocked cells in this experiment were not agglutinated, it is possible to exclude a "pseudo-blocking" phenomenon such as might conceivably be produced by the very close proximity of cells which had been agglutinated by the addition of a serum which was intended to block them. Our interpretation of these data is that the action of cross reacting antibody may be effectively blocked by prior occupation of the A or B antigen site by anti-A or anti-B. This clearly implies that the site of attachment of cross reacting antibody to the red cell is actually at the A or B antigen site. It is therefore necessary to conclude that the hypothetical C antigen either does not exist or that it exists as an integral property of the antigens A and B.

Further definition of the nature of cross reacting antibody may be sought through a consideration of the implications of the demonstration of the existence of asymmetric varieties of this antibody shown in tables 2, 3 and 4. If anti-"C" does in fact exist, it is necessary to propose some explanation for its apparent inability, in some cases, to function in a symmetric manner. Our experiments have demonstrated that cross reacting antibody exhibits the property of lattice formation in accordance with the theories of Marrack.* It is essential to the concept of lattice formation between two identical
antigens that the development of agglutinates be uninfluenced by the order in which the antibody combines with these two antigens. In other words, any explanation of cross reacting antibody on the grounds of the existence of a hypothetical antigen C, which is common to A and B cells, would necessarily lead to the conclusion that the antibody, anti-C, should invariably exhibit symmetric behavior. It should join group A cells to group B cells without regard to the order of attachment. As we have shown, some examples of cross reacting antibody exhibit a strong dependence, for their demonstration, on the order in which the lattice is built up. Because of this, we would contend that the concept of cross reacting antibody as being directed against an antigen which is common to A and B cells is not tenable. The results of the blocking experiment (Experiment 1) localized the physical site of action of the cross reacting antibody to the A and B antigen sites themselves. When these two sets of data are considered together the evidence becomes strongly favorable to the hypothesis that the cross reacting powers of group O serum are due to an antibody which combines the properties of anti-A and anti-B.

**Summary**

An account is given of an experiment in which the use of a "blocking" procedure has enabled the site of action of the cross reacting antibody in group O serum to be shown to be homologous with the A and B antigens of the red cell. In another experiment cross reacting antibody was shown to behave asymmetrically. In both these experiments use was made of the mixed agglutination technic for directly demonstrating the adherence of two cells of differing specificity by cross reacting antibody.

The significance of the results of these experiments is discussed in the light of observations by other workers.

**SUMMARIO IN INTERLINGUA**

Es reportate un experimento in que le uso de un technica de blocage permetteva le demonstration que le sito de action del anticorpore a reaction cruciate in sero del gruppo 0 es homologe con le antigenos A e B del erythrocyto. In un altere experimento il esseva monstrate que anticorpore a reaction cruciate se comporta asymmetricamente. In ambe iste experimentos le technica del agglutination mixte esseva utilitate pro demonstrar directemente le adherentia de duo cellulas de specificitate differente per medio de anticorpore a reaction cruciate.

Le signification del resultatos de iste experimentos es discutite in le lumine de observationes per altere investigatores.

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