Evaluation of Surface Markers on Normal Human Lymphocytes Containing Parallel Tubular Arrays: A Quantitative Ultrastructural Study

By Claire M. Payne and Lewis Glasser

Normal lymphocytes from the peripheral circulation represent a heterogeneous population of cells with different surface markers and different functions. Some of these lymphocytes contain cytoplasmic inclusions called parallel tubular arrays (PTA), which can only be identified with certainty under the electron microscope. It is not known whether this ultrastructurally defined lymphocyte constitutes the major cell type of the T-lymphocyte population, B-lymphocyte population, or third population of lymphocytes (i.e., K cells, L cells, M cells, null cells), or is unrelated to any of these immunologically defined lymphocyte subpopulations. The purpose of this study was to determine if this morphologically identifiable lymphocyte constitutes the major cell type of any of these three lymphocyte subpopulations. A quantitative ultrastructural analysis of PTA-lymphocytes was performed on a lymphocyte-enriched fraction using three surface marker assays commonly used to identify the three major populations. Spontaneous rosettes formed with sheep erythrocytes (E-rosettes) were used as a marker for T lymphocytes. Sheep erythrocytes sensitized with rabbit IgM antibody and coated with mouse complement (EAC-rosettes) were used as a marker for B lymphocytes. Human group O, type R,R2 erythrocytes sensitized with Ripley anti-CD serum to identify the Fc receptors (EA6,-rosettes) were used as a marker for the third population of lymphocytes. Light microscopic examination of the preparations obtained from five healthy subjects revealed the following mean percentage of reacted lymphocytes: 79.2% E-rosettes, 8.8% EAC rosettes, and 16% EA6-rosettes. Ultrastructural examination of 178 EA6-rosettes from the five subjects revealed that 89% of the central rosette-forming lymphocyte cross-sections contained PTA. In one subject, 96% of the central rosette-forming lymphocyte cross-sections contained PTA. In contrast, examination of 369 E-rosettes obtained from five healthy subjects revealed that only 3.4% of the central rosette-forming lymphocyte cross-sections contained PTA, and examination of 151 EAC-rosettes from four healthy subjects revealed that only 11.5% of the central rosette-forming lymphocyte cross-sections contained PTA. It was concluded that parallel tubular arrays are a morphological marker for a population of lymphocytes bearing Fc receptors for cytophilic antibody identified by the EA6-rosette assay and that the lymphocyte containing these inclusions constitutes the major cell type of the third population of lymphocytes. The possible inclusion of the PTA-lymphocyte within other lymphocyte populations and within the monocyte population is discussed.

It has been well documented that normal lymphocytes from the peripheral circulation represent a heterogeneous population of cells with different surface markers and different functions.1-4 The two-component concept or duality of the immune system5 is gradually being replaced by a three-component concept after a third major population of lymphocytes was identified in mice6-9 and later in humans.10-12 This third population of cells is characterized by the presence of Fc receptors that bind cytophilic antibody and have been variously described as K cells,14 L cells,15-17 M cells,18 and null cells.19

Normal lymphocyte subpopulations present in the peripheral circulation cannot be identified morphologically by light microscopy. Although some investigators report successful separation of populations using cytochemistry, there are conflicting reports regarding the specificity of these findings.20 Ultrastructural differences have been noted using transmission electron microscopy,21-23 however, these differences are subtle and do not define homogeneous subpopulations of cells. Scanning electron microscopy initially showed microvilli on B lymphocytes and a smooth surface on T lymphocytes,24 but subsequent studies have shown this difference to be a preparative artifact.25 Further studies using scanning electron microscopy indicated that T and B lymphocytes do have subtle but nevertheless discernable differences in surface morphology.26 It is possible to demonstrate an abundance of rough endoplasmic reticulum in some B cells.27,28 This represents, however, a stage of differentiation following B-cell activation and is not seen in the majority of normal circulating B lymphocytes. Some human lymphocytes contain unique cytoplasmic inclusions called parallel tubular arrays that may be visible as nonspecific azurophilic granules on blood smears stained with Romanowsky dyes. These inclusions can only be identified with certainty under the electron microscope. The purpose of this article is to determine if this morphologically identifiable lymphocyte constitutes the major cell type of the T lymphocyte, B lympho-
cyte, or third population of lymphocytes. A quantitative ultrastructural analysis of lymphocyte rosettes was performed using three different surface marker assays commonly used to identify these three major populations. We conclude that parallel tubular arrays are a morphological marker for a population of lymphocytes bearing Fc receptors for cytotoxic antibodies identified by the EA<sub>M</sub>-rosette assay. The lymphocyte containing these inclusions by definition constitutes the major cell type of the third population of lymphocytes. The possible inclusion of the PTA-lymphocyte within other lymphocyte populations and within the monocyte population is discussed.

MATERIALS AND METHODS

**Lymphocyte Isolation**

Peripheral blood samples were collected by venipuncture from 5 healthy adults (3 female, 2 male) and drawn into heparinized evacuated test tubes. Whole blood was separated by Ficoll-Hypaque density gradient centrifugation (sp. gr. 1.077). The mononuclear fraction at the interface was removed and incubated at 37°C for 30 min with Lymphocyte Separator Reagent (Technicon Instrument Corp., Tarrytown, N.Y.) which contains micron-sized magnetic particles sensitized with poly L-lysine. Following incubation, the cells were passed through tygon tubing wrapped around a magnet that effectively removed iron-laden phagocytes and excess iron filings. The final lymphocyte-rich preparations had viabilities ranging from 96% to 99% (mean 97.2%) as measured by eosin dye exclusion, recoveries ranging from 76% to 83% (mean 79%), and lymphocyte purities ranging from 95% to 98% (mean 96.6%).

**Preparation of E-Rosettes**

Spontaneous rosette formation using sheep erythrocytes was prepared according to methods previously described. Sheep red blood cells (SRBC) were suspended in Alsever's solution. Fetal calf serum (FCS) was absorbed with sheep erythrocytes at 4°C and 37°C inactivated at 56°C. A 2% SRBC suspension in Hanks' balanced salt solution (0.25 ml), FCS (0.25 ml), and 0.50 ml of lymphocytes (10<sup>6</sup>/ml) were incubated for 15 min at 37°C, pelleted at 200 g, and incubated overnight at 4°C. Normal values in our laboratory range from 62% to 86% with a mean of 78%.

**Preparation of EAC-Rosettes**

Sheep erythrocytes were sensitized with rabbit IgM antibody (Cordis Laboratories, Miami, Fla.) at room temperature using half the minimum agglutinating titer and then coated with freshly prepared absorbed whole mouse complement (EAC-SRBC) at 37°C. A 0.5-ml suspension of lymphocytes (10<sup>7</sup>/ml) and 0.5-ml suspension of 1% EAC-SRBC were incubated at 37°C with continuous mixing for 30 min. Normal values in our laboratory range from 4% to 12% with a mean of 8%.

**Preparation of E<sub>M</sub>-Rosettes**

Human group O, type R<sub>1</sub>R<sub>2</sub> erythrocytes were sensitized with Ripley anti-CD serum. The titer of the antiserum was 1:80,000. Equal volumes of suspensions of 1% sensitized R<sub>1</sub>R<sub>2</sub> erythrocytes and lymphocytes (10<sup>7</sup>/ml) were centrifuged for 5 min at 200 g and tubes placed upright at room temperature for 30 min. Normal values in our laboratory range from 8% to 25% with a mean of 15%.

**Preparation of Rosettes for Electron Microscopy**

Rosettes were initially fixed in suspension with 1.5% glutaraldehyde in 0.1 M phosphate buffer (pH 7.2) for stabilization and later spun in large round-bottomed plastic tubes as previously described. The resulting pellets were postfixed in 1% osmium tetroxide in 0.1 M phosphate buffer, dehydrated through a graded series of ethanol, and embedded in Spurr's epoxy. One-micron sections were cut and stained with toluidine blue and examined with the light microscope. Those blocks containing numerous rosettes were selected and ultrathin sections were cut with a diamond knife on a Sorvall MT2-B ultramicrotome and mounted on uncoated, 200-mesh copper grids. The ultrathin sections were stained with lead citrate and uranyl acetate and then lightly carbon-coated before examination with a Hitachi HU-12 electron microscope.

**Quantitation of Rosettes by Light and Electron Microscopy**

In the E-rosette and EAC-rosette preparations, a rosette was defined as a lymphocyte with three or more attached erythrocytes. In the EA<sub>M</sub>-rosette preparations, a rosette was defined as a lymphocyte with five or more attached erythrocytes. One-hundred rosettes were scored in each preparation examined by light microscopy. A minimum of 26 rosettes was scored in each rosette preparation examined by electron microscopy. A PTA-lymphocyte was defined as a lymphoid cell containing at least one cytoplasmic inclusion that could be identified as a parallel tubular array at high magnification. The cytoplasm of each central rosette-forming lymphocyte was examined through the attached 10X ocular system at a scope magnification of 10,000X. This close examination was found necessary—since parallel tubular arrays that are not membrane-bound can have a similar electron density as the surrounding cytoplasm—and be easily missed at a low magnification.

The percentages of PTA-lymphocytes scored in each rosette preparation are an underestimate of the true value since an ultrathin section taken for electron microscopy constitutes only a small fraction of the total cell volume.

**Preparation of Unfractionated Whole Blood for Electron Microscopy**

Theuffy coats from 16 normal subjects were prepared for electron microscopy by centrifuging whole blood in Wintrobe tubes, removing the plasma, and immediately fixing the cells as previously described.

**RESULTS**

The five volunteers chosen for this study had normal hematologic values. The white blood cell counts had a mean of 6300 with a range of 3500–9900. The mean percentage of lymphocytes was 29.8 with a range of 23–38. The mean absolute lymphocyte count was 1762/µl with a range of 1216–2574/µl.

Light microscopic analysis of the three different rosette preparations (Table 1) gave results comparable to those previously described. The mean percentage of E-rosettes was 79 with a range of 72–86. The mean absolute number of E-rosetting cells was 1415/µl with a range of 876–2162/µl (Table 2). The mean percentage of EAC-rosettes was 8.8 with a range of 5–12. The mean absolute number of EAC-rosetting cells was 140/µl with a range of 61–237/µl. The mean
percentage of EA<sub>hu</sub>-rosettes was 16 with a range of 8–25. The mean absolute number of EA<sub>hu</sub>-rosetting cells was 270/μl with a range of 137–412/μl.

Ultrastructural analysis of the percentage of central rosette-forming cells containing parallel tubular arrays (PTA-lymphocyte-rosettes) revealed that the majority of the EA<sub>hu</sub>-rosettes had PTA-lymphocytes as the central rosette-forming cell (Table I, Fig. 1). The mean percentage of PTA-lymphocyte-EA<sub>hu</sub>-rosettes was 89.0 ± 7.0 (SD) with a range of 76–96. The mean percentage of PTA-lymphocyte-E-rosettes was only 3.4 ± 2.6 (SD) with a range of 0–7. The mean percentage of PTA-lymphocyte-EAC-rosettes was slightly higher than that of the E-rosettes with a mean of 11.5 ± 1.5 SD and a range of 9–13. The mean absolute number of PTA-lymphocyte-E-rosettes was 58/μl with a range of 0–130/μl. The mean absolute number of PTA-lymphocyte-EAC rosettes was 15/μl with a range of 7–21/μl. The mean absolute number of PTA-lymphocyte-EA<sub>hu</sub>-rosettes was 241/μl with a range of 121–396/μl. Except for the absence of parallel tubular arrays in some of the planes of section, the lymphocytes at the center of the EA<sub>hu</sub>-rosettes appeared ultrastructurally similar in any given subject and from subject to subject.

In order to determine if the rosetting procedure, and in particular the EA<sub>hu</sub>-rosette assay, induced the formation of parallel tubular arrays, the absolute number of PTA-lymphocytes determined after rosetting was compared to the absolute number of PTA-lymphocytes determined from unfractionated buffy coat preparations. The mean absolute number of PTA-lymphocytes determined after adding up the PTA-lymphocyte E-, EA<sub>hu</sub>, and EAC rosettes was 257 ± 84.7/μl. The mean absolute number of PTA-lymphocytes determined from unseparated buffy coat preparations was 328 ± 118.7/μl. Although there were less PTA-lymphocytes in the purified and rosetted lymphocyte fractions, this decrease was not statistically significant.

**DISCUSSION**

Parallel tubular arrays (PTA) are ultrastructurally distinct inclusions found in the cytoplasm of some lymphocytes. These inclusions have not been observed in any other hematopoietic or nonhematopoietic cell. We have previously shown that normal peripheral blood lymphocytes containing PTA behave as a distinct population of cells when challenged with glucocorticoids. A question we now propose to answer is to what population of lymphocytes do these ultrastructurally distinct cells belong: the B-lympho-

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**Table 1. Percentage of Central Rosette-Forming Cells Containing Parallel Tubular Arrays in Normal Human Lymphocyte Populations**

<table>
<thead>
<tr>
<th>Volunteer</th>
<th>Percent PTA-Lymphocytes† as CRFC in E-Rosettes</th>
<th>Percent PTA-Lymphocytes† as CRFC in EAC-Rosettes</th>
<th>Percent EA&lt;sub&gt;hu&lt;/sub&gt;-Rosettes†</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>74 (38)</td>
<td>12 (31)</td>
<td>18 (29)</td>
</tr>
<tr>
<td>2</td>
<td>72 (44)</td>
<td>5 (34)</td>
<td>25 (42)</td>
</tr>
<tr>
<td>3</td>
<td>86 (180)</td>
<td>6 (51)</td>
<td>8 (33)</td>
</tr>
<tr>
<td>4</td>
<td>80 (41)</td>
<td>9 (35)</td>
<td>13 (48)</td>
</tr>
<tr>
<td>5</td>
<td>84 (66)</td>
<td>ND</td>
<td>16 (26)</td>
</tr>
</tbody>
</table>

* Determined by light microscopy.
† Lymphocytes whose cellular cross-sections contained parallel tubular arrays.
§ Central rosette-forming cell.
§ Numbers in parentheses indicate the total number of rosette cross-sections examined under the electron microscope.

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**Table 2. Absolute Numbers of Central Rosette-Forming Cells Containing Parallel Tubular Arrays in Normal Human Lymphocyte Populations**

<table>
<thead>
<tr>
<th>Volunteer</th>
<th>E-rosettes/μl</th>
<th>PTA-Lymphocyte E-Rosettes/μl†</th>
<th>EAC-Rosettes/μl</th>
<th>PTA-Lymphocyte EAC-Rosettes/μl</th>
<th>EA&lt;sub&gt;hu&lt;/sub&gt;-Rosettes/μl</th>
<th>PTA-Lymphocyte EA&lt;sub&gt;hu&lt;/sub&gt;-Rosettes/μl</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>984</td>
<td>0</td>
<td>159</td>
<td>21</td>
<td>239</td>
<td>222</td>
</tr>
<tr>
<td>2</td>
<td>876</td>
<td>18</td>
<td>61</td>
<td>7</td>
<td>304</td>
<td>231</td>
</tr>
<tr>
<td>3</td>
<td>1,471</td>
<td>29</td>
<td>103</td>
<td>12</td>
<td>137</td>
<td>121</td>
</tr>
<tr>
<td>4</td>
<td>1,582</td>
<td>111</td>
<td>237</td>
<td>21</td>
<td>257</td>
<td>236</td>
</tr>
<tr>
<td>5</td>
<td>2,162</td>
<td>130</td>
<td>ND</td>
<td>ND</td>
<td>412</td>
<td>396</td>
</tr>
</tbody>
</table>

* Determined from light microscopic results.
† Determined from electron microscopic results.
cyte population, T-lymphocyte population, or the third population of lymphocytes (i.e., K cells, L cells, M cells, null cells)? Previous studies have failed to unequivocally determine the true identity of PTA-lymphocytes. Brunning and Parkin15 and McKenna et al.36 in a study of a chronic lymphoproliferative disorder and McKenna et al.37 in a study of infectious mononucleosis, described PTA-lymphocytes in E-rosettes and concluded that the PTA-lymphocyte is most probably a T lymphocyte. The identity of the PTA-lymphocyte as simply a subset of T lymphocytes was challenged when Payne et al.,38 in a study of severe combined immunodeficiency disease, identified PTA-lymphocytes in both E- and EAC-rosettes. Since the EAC-rosette has been criticized as measuring both Fc receptors and complement receptors, Payne and Nagle39 identified true complement receptors on PTA-lymphocytes from the normal peripheral circulation.
using an assay system that circumvents the use of antibody and activates complement by the alternate pathway. Appay et al., in a study of six normal subjects, could not detect surface immunoglobulin on PTA-lymphocytes using anti-human IgM peroxidase-labeled Fab\(_2\) fragments. They concluded that the lymphocytes containing these “bundle-shaped tubular (BST) inclusions” are not B lymphocytes, but they could not determine if they belonged to T cells and/or to the third lymphocyte population. This observation is consistent with the reported absence of PTA in the neoplastic cells of proven B-cell-derived neoplasms.\(^{35,36}\)

In this study, a quantitative analysis of the central rosette-forming cell using three assays commonly used to distinguish the three major populations has revealed that the PTA-lymphocytes constitute the major cell type of the third population of lymphocytes. This was evidenced by the fact that 89% of the EA\(_{hu}\)-rosettes, used as a marker for the third population, were formed by PTA-lymphocytes in contrast to only 3% of the E-rosettes and 12% of the EAC-rosettes. It is noteworthy that in one subject, 96% of the EA\(_{hu}\)-rosette cross-sections contained parallel tubular arrays (Table 1). In order to determine if the rosetting procedure, and in particular the EA\(_{hu}\)-rosette assay, induced the formation of parallel tubular arrays, the absolute number of PTA-lymphocytes determined in the rosetted preparations was compared to the absolute number of PTA-lymphocytes determined from unseparated buffy coat preparations. Although there was a 22% decrease in the number of PTA-lymphocytes in the rosetted preparations, this decrease was not statistically significant. The loss in PTA-lymphocytes in the purified and rosetted fractions may be a reflection of the 21% loss in total lymphocytes resulting from the isolation procedure. The parallel tubular array can therefore be used as a morphological marker for the third population of lymphocytes that bear Fc receptors for cytophilic antibodies identified by the EA\(_{hu}\)-rosette assay. The finding of a small percentage of PTA-lymphocytes in E- and EAC-rosetting preparations can be explained by the lack of specificity of these surface marker assays or the inclusion of parallel tubular arrays in other minor subpopulations. Although most E-rosetting lymphocytes are of T-cell origin,\(^{30}\) a small percentage include third population cells.\(^{1,2,41}\) Lymphocytes known to form EAC-rosettes include not only B lymphocytes\(^{32,42}\) but third population cells\(^{1,2,41}\) as well.

The finding of Fc receptors on PTA-lymphocytes is consistent with the finding of Huhn et al.,\(^{45}\) who demonstrated Fc-receptors using soluble peroxidase-anti-peroxidase (PAP) complexes. They stated that two different types of lymphocytes with strong PAP-labeling of their membranes were recognized. The first subgroup of strongly PAP-positive lymphocytes showed a low degree of morphological differentiation, and the second subgroup contained parallel tubular arrays. This is in contrast to our finding in which the Fc receptor-bearing lymphocytes identified by means of the EA\(_{hu}\)-rosette assay appeared to represent a morphologically homogenous cell population, most of which could be determined to contain parallel tubular arrays. Perhaps the EA\(_{hu}\)-rosette-forming lymphocytes correspond to the antibody-dependent cytotoxic lymphocytes (ADCL), and the agg-Ig-positive lymphocytes identified by the use of PAP complexes represent two or more functionally distinct lymphocytes (i.e., a subpopulation of T lymphocytes and/or B lymphocytes having Fc receptors and ADCL).

Other work from our laboratory and elsewhere support the concept that the PTA-lymphocytes are antibody-dependent cytotoxic lymphocytes. We have shown that after the in vivo administration of dexamethasone, the percentage of PTA-lymphocytes\(^{34}\) and the percentage of EA\(_{hu}\)-rosettes\(^{46}\) increased significantly in the peripheral circulation, whereas the absolute number of each remained essentially unchanged. This insensitivity to steroids may indicate that these cells have fewer glucocorticoid receptor sites than other lymphocyte populations. The postdexamethasone lymphocyte population was analyzed functionally by Parrillo and Fauci.\(^{47}\) They showed that there was a significant increase in antibody-dependent cell-mediated cytotoxicity by the poststeroid population.

The finding of a small percentage of E- and EAC-rosettes containing parallel tubular arrays is not inconsistent with the concept that the PTA-lymphocytes are “killer” cells exhibiting antibody-dependent cytotoxicity. West et al.\(^{41}\) found that low affinity E-rosette-forming cells were highly enriched for cytotoxic reactivity against antibody-sensitized Chang liver cells, whereas high-affinity E-rosette-forming cells contained few antibody-dependent cytotoxic cells (K cells). It is also known that in addition to B lymphocytes,\(^{32,42}\) complement receptors can be detected on antibody-dependent cytotoxic lymphocytes.\(^{1,44}\) It is not possible in the experimental design used in the present study to determine if all three surface markers are found on the same PTA-lymphocyte. Determination of absolute PTA-lymphocyte-rosette counts (Table 2) has shown that if these surface markers represent three mutually exclusive subpopulations, there are four times as many PTA-lymphocyte EA\(_{hu}\)-rosetting cells as PTA-lymphocyte E-rosetting cells in the peripheral circulation and 16 times as many PTA-lymphocyte EA\(_{hu}\)-rosetting cells as PTA-lymphocyte
EAC-rosetting cells. This seems to indicate that although all lymphocytes bearing Fc receptors for cytophilic Ripley antibody appear to be PTA-lymphocytes, fewer PTA-lymphocytes seem to form E-rosettes and even less have complement receptors. E-rosetting PTA-lymphocytes may include Tγ cells, since Fc receptors for Ripley-equivalent antibodies have been demonstrated on their surface. The relationship between third population lymphocytes and Tγ cells has not been completely elucidated. Functionally, both third population lymphocytes and Tγ cells express killer-cell activity. Of interest is the finding of cytoplasmic azurophilic granules in Tγ cells by light microscopy. Electron microscopy did show numerous cytoplasmic granules, but these granules did not have the typical ultrastructural appearance of parallel tubular arrays. The relationship between the granules seen in Tγ cells and the parallel tubular arrays seen in EAhu-rosette-forming cells requires further study.

The complement receptors on PTA-lymphocytes are most likely C3b, since these receptors have been identified on third population cells. It is unlikely that C3d receptors are found on PTA-lymphocytes, since these receptors are restricted to B lymphocytes, and Appay et al. have shown that PTA-lymphocytes are not B lymphocytes.

The cells containing parallel tubular arrays have ultrastructural and cytochemical features of lymphocytes but are atypical in some respects. Recent studies by Kay and Horwitz using OKMI antibodies question the lymphoid origin of the effector cells involved in antibody-dependent cellular cytotoxicity. They concluded, however, that the cells were probably not monocytes. We have been unable to demonstrate peroxidase activity in PTA-lymphocytes and thus far have been unable to demonstrate either monocytic or granulocytic enzymatic differentiation. We have shown, however, some functional differentiation by demonstrating that some PTA-lymphocytes phagocytize complement-coated bacteria.

Experimental evidence to date indicates that PTA-lymphocytes do not possess surface immunoglobulins, have no endogenous peroxidase activity, and constitute the majority of the EAhu-rosette-forming cells. At least some PTA-lymphocytes form E-rosettes and have complement receptors. PTA-lymphocytes have been determined to be steroid-resistant and apparently do not recirculate when challenged with glucocorticoids. From a pathologic standpoint, PTA-lymphocytes constitute a major portion of the circulating lymphocytes in patients with severe combined immunodeficiency, increase in numbers in infectious mononucleosis, and may become neoplastic.

In conclusion, we have shown that lymphocytes containing parallel tubular arrays do not represent the major cell type of the T- or B-lymphocyte population. PTA-lymphocytes do, however, represent the major cell type of the third population of lymphocytes. It is our opinion that the parallel tubular array can be used as a morphological marker for this lymphocyte population, which contains Fc receptors for cytophilic antibody identified by the EAhu-rosette assay. Future experimentation is necessary to determine the ontogeny of the PTA-lymphocyte and the functional significance of parallel tubular arrays in the physiology and/or immunology of these ultrastructurally distinct cells.

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