The Specific Acylation of Glycerol 3-Phosphate to Monoacylglycerol 3-Phosphate in Escherichia coli

EVIDENCE FOR A SINGLE ENZYME CONFERRING THIS SPECIFICITY*

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TAPAS K. RAY, JOHN E. CRONAN, JR.,† RICHARD D. MAVIS,§ AND P. ROY VAGELOS

From the Department of Biological Chemistry, Washington University School of Medicine, St. Louis, Missouri 63110

SUMMARY

Pronounced positional specificity during the acylation of glycerol 3-phosphate to form monoacylglycerol 3-phosphate has been shown with a particulate enzyme preparation from Escherichia coli. Palmitic acid is found to be esterified exclusively to position 1 while unsaturated fatty acids are predominantly esterified to position 2. Evidence for a single enzyme being involved in this specific acylation is presented. This evidence is based on studies of single site mutants of E. coli possessing a glycerol 3-phosphate acyltransferase of greatly increased thermolability and on chemical modification of the enzyme. Additional experiments show that the acylation of 1-acylglycerol-3-P involves an enzyme activity or activities separate from that which acylates glycerol-3-P.

Phosphoglycerides play an important role in the structure and function of all biological membranes (1-5). In most naturally occurring phosphoglycerides unsaturated fatty acids are preferentially esterified at position 2 and saturated fatty acids at position 1 of the glycerol molecule (2). This asymmetric fatty acid distribution is thought to be of major importance in the functional and structural role of phosphoglycerides in membrane processes. Perturbations in the asymmetric distribution of the fatty acids of membrane phosphoglycerides can produce drastic disturbances in cellular physiology (6-13). Thus the enzymatic mechanisms conferring such positional specificity of fatty acid residues are of central importance to the cell. A likely origin of this asymmetric distribution of fatty acids would be the esterification of glycerol-3-phosphate to form phosphatidic acid, a key intermediate in the biosynthesis of the phospholipids.

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† Postdoctoral Fellow of the National Institute of General Medical Sciences (1-F02-GM 34773-02). Address as of December 1, 1970, Department of Molecular Biophysics and Biochemistry, Yale University, New Haven, Connecticut 06520.
§ Postdoctoral Fellow of the National Heart Institute (1-F02-HE-34,846-01).

MATERIALS AND METHODS


glycerol 3-phosphate to form monoacylglycerol 3-phosphate. Early studies on the positional substrate specificity of glycerol 3-phosphate acyltransferase in liver microsomal systems (14-16) indicated that glycerol 3-phosphate was acylated in a nearly random manner, although marked positional specificity was exhibited in the esterification of 1- and 2-acylglycerol 3-phosphates (17) or at least in the esterification of 1-acylglycerol-3-P (18). However, several subsequent investigations with the enzyme from rat liver have shown that glycerol 3-P acylation proceeds in a nonrandom, asymmetric manner, so that unsaturated fatty acids are preferentially esterified at position 2 of the phosphatidic acid (19-21). Some of these studies have reported monoacylglycerol-3-P as an intermediate in this reaction (22-25). A recent report of van den Bosch and Vagelos (25) has shown that acylation of glycerol-3-P by a particulate enzyme system in Escherichia coli proceeds with similar preferential positioning of saturated and unsaturated fatty acids. In the present study, we have used our collection of E. coli strains possessing a mutation in glycerol-3-P acyltransferase (26) to produce evidence that a single enzyme catalyzes the positionally specific acylation of glycerol-3-P by either saturated or unsaturated fatty acyl coenzyme A substrates to form monoacylglycerol-3-P. We also present evidence that this enzyme is distinct from that activity which acylates 1-acylglycerol-3-P to form phosphatidic acid.
phosphatidic acid, monoacylglycerol 3-P, and monoglyceride on silica gel thin layer plates impregnated with NaCO₃ according to the method of Hajra and Agranoff (37) with chloroform-methanol-acetone-acetic acid-water (200:80:30:40:20 v/v) as the developing solvent. The identity of the various lipids was ascertained by cochromatography with authentic standards. The lipids were located by iodine vapor and the appropriate areas of silica gel were scraped from the plate. The silica gel was then eluted with 10 ml of chloroform-methanol (1:4 v/v) for further analysis, and aliquots were counted in Bray's solution (38) after evaporation to dryness under a stream of nitrogen. Alternatively, the radioactivity was measured by suspending the scrapings from the silica gel plate into toluene scintillation solution containing 3.5% thixotropic gel (Cab-O-Sil, Packard Instruments, Downers Grove, Illinois). All counting was done in a Packard 3380 scintillation counter.

Analysis of Monoacylglycerol-3-P—Monoacylglycerol-3-P was at least 80 to 85% degraded to monoglyceride by phosphatidic acid phosphatase prepared from rat liver and utilized as described by Wilgram and Kennedy (39), except that the reaction mixture contained additional 0.05 M borate buffer to prevent migration of acyl groups. The monoglycerides thus formed were fractionated into the 1- and 2-isomers on bovine impregnated silica gel thin layer plates with Solvent Systems A and F of Thomas, Scharoun, and Ralston (40) and quantitatively determined by counting the appropriate areas of silica gel in Bray's solution. A number of saturated and unsaturated monoglycerides were tested in these systems to ascertain that the degree of saturation of the acyl portion of the monoglyceride has no effect on the separation. The monoglycerides formed were further characterized by elution from silica gel and treatment (41) with porcine pancreatic lipase from Worthington.

Free fatty acids and monoglycerides from the lipase digestions were separated on silica gel plates according to the method of Freeman and West (42) and assayed for radioactivity.

RESULTS

Specificity in Acylation of Glycerol-3-P to Monoacylglycerol-3-P—Fig. 1 shows the time course of the acylation of glycerol-3-P with either palmitoyl-CoA or oleyl-CoA as the acyl donor. The total of the three products of the acylation reaction, monoglyceride, monoacylglycerol-3-P, and phosphatidic acid, is stoichiometric with the release of free CoA as measured in the spectrophotometric assay. Previous reports from this laboratory (22, 25) have shown that the relative amounts of the three products formed in vitro is dependent on the experimental conditions employed. The pH of the incubation mixture is especially important since the acylation reaction which produces monoacylglycerol-3-P, the reaction which acylates 1-acylglycerol-3-P, and the phosphatase which dephosphorylates monoacylglycerol-3-P to monoglyceride, all have distinctly different pH optima. The acylation reaction which forms monoacylglycerol-3-P is linear for at least 10 min as was the release of free CoA as determined spectrophotometrically. However the formation of monoglyceride and phosphatidic acid cease after about 4 to 6 min of reaction. The relative amounts of monoacylglycerol-3-P, phosphatidic acid, and monoglycerides formed during the acylation of glycerol-3-P with either palmitoyl-CoA (Fig. 1A) or oleyl-CoA (Fig. 1B) are very similar. Thus with either of these substrates, we can obtain conditions under which monoacylglycerol-3-P is the major product of the reactions.
Acylglycerol-3-P formed by incubation of radioactive glycerol-3-P was rigorously examined for this specificity. The species of monoacyl lipids during extraction and chromatography. Thus we have been able to make a more comprehensive study of the acylation process.

We have extended these observations with conditions designed to maximize the accumulation of monoacylglycerol-3-P and to minimize the migration of the acyl moieties between the two isomeric monoglycerides separated by borate-impregnated silica gel thin layer chromatography (see "Materials and Methods").

Preliminary results of van den Bosch and Vagelos (25) have been shown that the acylation of glycerol-3-P with palmitoyl-CoA was exclusive. In contrast, when oleyl-CoA was used as the acyl donor in an identical system, acylation of position 1 predominated. These data suggested that the acylating system possessed the ability to discriminate between saturated and unsaturated fatty acids and also between the two isomeric monoglycerides separated by borate-impregnated silica gel thin layer chromatography (see “Materials and Methods” for further details).

![Graph A](image1.png)

**Fig. 1.** Time course of acylation reactions. Glycerol 3-phosphate acyltransferase assay mixtures containing strain 8 enzyme preparation (100 μg of protein), [14C]-glycerol-3-P (1 mCi per mmole), and either 30 μM palmitoyl-CoA (A) or 30 μM oleyl-CoA (B) in a total volume of 0.2 ml were incubated at 25°. At various times samples were taken and the lipids extracted. The lipids were then separated into monoacylglycerol-3-P, O—O; phosphatic acid, Δ—Δ; and monoglyceride Δ—Δ, fractions and their radioactivity determined (see “Materials and Methods” for further details).

### Table I

**Specificity in acylation of glycerol 3-phosphate by particulate preparation of strain 8**

The standard assay mixture for glycerol-3-P acylation was used except that uniformly labeled [14C]-glycerol-3-P (final specific activity 1 mCi per mmole) was added and the various acyl-CoA's were added at the indicated concentrations, which were found to give maximal activity in the spectrophotometric assay. After incubation for 10 min at 25° the reaction mixtures were extracted and the monoacylglycerol-3-P fractions were isolated, dephosphorylated with phosphatidic acid phosphatase, and the resulting isomeric monoglycerides separated by borate-impregnated silica gel thin layer chromatography (see “Materials and Methods”).

| Acyl donor       | Acyl-CoA concentration | Total monoacylglycerol-3-P treated with phosphatase | Recovered monoglyceride | Percentage of total recovered monoglyceride as 1-acylglycerol |
|------------------|------------------------|---------------------------------------------------|-------------------------|-------------------------------------------------------------|
|                  | μM | mmole | mmole | 1-Acylglycerol | 2-Acylglycerol |
| experiment 1     |    |       |       |              |              |
| Palmitoyl-CoA    | 30 | 1.7   | 1.0   | 0.12         | 92            |
| Oleyl-CoA        | 30 | 5.5   | 5.1   | 1.4          | 8             |
| Palmityl-CoA     | 5  | 1.53  | 0.23  | 1.14         | 17            |
| Stearyl-CoA      | 10 | 1.82  | 0.33  | 1.23         | 3             |
| cis-Vaccenyl-CoA | 5  | 1.49  | 0.15  | 1.14         | 12            |
| Myristyl-CoA     | 5  | 1.09  | 0.17  | 0.61         | 37            |
| experiment 2     |    |       |       |              |              |
| Palmitoyl-CoA    | 30 | 2.8   | 1.8   | 0.05         | 98            |
| Oleyl-CoA        | 30 | 3.0   | 3.3   | 2.5          | 12            |
| Stearyl-CoA      | 10 | 2.3   | 0.14  | 1.15         | 28            |
| experiment 3     |    |       |       |              |              |
| Palmitoyl-CoA    | 30 | 6.2   | 5.5   | 0.30         | 95            |
| Oleyl-CoA        | 30 | 4.2   | 3.5   | 0.30         | 10            |

### Table II

**Pancreatic lipase treatment of isomeric monoglyceride fractions**

Glycerol-3-P acylation reaction mixtures were incubated with an enzyme preparation from strain 8 as in Table I with [14C]-labeled glycerol-3-P and either palmitoyl-CoA or oleyl-CoA as substrates. The monoglycerides were obtained by dephosphorylation of the monoacylglycerol-3-P fraction resulting from the incubation with phosphatidic acid phosphatase and chromatography on a borate-impregnated silica gel thin layer plate with solvent System A of Thomas et al. (40). The fractions designated 1-monoglyceride and 2-monoglyceride were identified by co-chromatography with authentic standards. The 1-monoglyceride fraction resulting from the palmitoyl-CoA incubation and the 2-monoglyceride fraction resulting from the oleyl-CoA incubation were then eluted from the silica gel with chloroform. The chloroform was evaporated under nitrogen and the monoglyceride fractions were incubated with pancreatic lipase. After incubation the mixture was fractionated into chloroform- and water-soluble fraction by the method of Bligh and Dyer (36). The degree of hydrolysis was ascertained by counting both the chloroform- and the water-soluble products (see “Materials and Methods” for further details).

| Chromatographic monoglyceride fraction | [14C]-glycerol-labeled monoglyceride treated with pancreatic lipase | Counts recovered in |
|---------------------------------------|---------------------------------------------------------------------|---------------------|
|                                       | CHCl3 phase | Water phase |
| 1-Monoglyceride                       | 6500 cpm    | 40 cpm  | 6100 cpm |
| 2-Monoglyceride                       | 2500 cpm    | 2300 cpm| 30 cpm   |
3-P with various acyl-CoA's were treated with phosphatidic
acid phosphatase and the resulting monoglycerides were
separated into their 1- and 2-isomers by thin layer chromatography. As
seen in Table I all unsaturated fatty acids tested are predomin-
antly esterified to position 2 while palmitic acid is almost
completely esterified to position 1. Myristic and stearic acids,
the other saturated acyl-CoA's tested, are found to be distributed
between both positions with position 2 predominating. The
identity of the isomeric monoglycerides isolated and identified by
thin layer chromatography was confirmed by treatment with
pancreatic lipase. Pancreatic lipase is known to have an ab-
solute specificity for position 1 since it hydrolyzes 1-mono-
glyceride completely but has no effect on 2-monoglyceride (43).
As shown in Table II, dephosphorylation of the product of a
reaction mixture containing palmityl-CoA produced material
which cochromatographed with authentic 1-monoglyceride and
released 14C-glycerol into the aqueous phase when treated with
pancreatic lipase. In contrast, dephosphorylation of the product
of a reaction containing oleyl-CoA produced material which
cochromatographed with 2-monoglyceride and was not hy-
drolyzed by pancreatic lipase. Thus it was apparent that this
particulate enzyme system was able to acylate glycerol-3-P to
monoacylglycerol-3-P in a highly specific asymmetric manner.
We next attempted to understand the enzymatic basis of this
specificity, i.e. does this specific acylation require more than one
enzyme?

Evidence for Single Enzyme Involved in Specific Acylation of
Glycerol-3-P—We have previously described the isolation of
temperature-sensitive strains of E. coli possessing a mutant
glycerol-3-P acyltransferase of greatly increased thermolability
(20). Several other mutants were subsequently isolated. The
first mutant described was called CV15; two other mutants,
CV2 and CV31, have also been studied in detail. These mutants
were all independently isolated and their reversion frequencies
to temperature resistance are consistent (44) with their phenotype
being the result of single mutations in the structural gene for
the acyltransferase. In addition the transduction frequency to
temperature resistance for CV16 obtained with Phage PIKc
grown on strain 8 is consistent with the phenotype of CV15
being caused by a single mutation (44).

Figs. 2 and 3 show the kinetics of the thermal inactivation of
glycerol-3-P acyltransferase activities of particulate preparations
derived from these mutants and their parent, strain 8, with
either saturated or unsaturated acyl-CoA's as acyl donors. It
is apparent in Fig. 2, where glycerol-3-P acyltransferase ac-
tivities of Mutants CV15 and CV31 were studied, that the rate
of thermal inactivation of the enzyme is similar in these two
mutants (half-life of 17 min for CV15, 18+ min for CV31). More
important, however, is the finding that the thermolability of the
activity with either palmityl-CoA or oleyl-CoA as acyl donor is
identical in enzyme preparations from a given mutant. A
more detailed study was done of Mutant CV2 and wild type,
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FIG. 4. Effect of maleic anhydride treatment on the glycerol-3-P acyltransferase and 1-acylglycerol-3-P acyltransferase activities of strain 8. An enzyme preparation of strain 8 was treated with various amounts of maleic anhydride as described under "Materials and Methods." The maleylated preparations were then assayed spectrophotometrically for both glycerol-3-P acyltransferase and 1-acylglycerol-3-P acyltransferase activities with either palmityl-CoA or oleyl-CoA. The data are expressed relative to an untreated sample of the preparations (= 100%). Typical specific activities of 1-acylglycerol-3-P acyltransferase of the unheated sample of strain 8 are 4.2 and 6.7 with palmityl-CoA and oleyl-CoA, respectively, as acyl donor. ○ and ■ denote glycerol-3-P acyltransferase activity; □ and □ denote 1-acylglycerol-3-P acyltransferase activity. Activities with either palmityl-CoA (○ and ○) or oleyl-CoA (■ and □) are shown.

strain 8, with several additional acyl-CoA's. Fig. 3 indicates that the enzyme preparation of CV2 (half-life 9 min) is much more thermostable than either the parent, strain 8, or Mutants CV15 and CV31 (see Fig. 2). Again it is noted that the rate of enzyme inactivation is the same in either of these two strains whether the saturated acyl donors, stearyl-CoA and palmityl-CoA, or unsaturated acyl donors, oleyl-CoA, cis-vaccenyl-CoA and palmitoleyl-CoA, are used as substrates. In addition the experiments of Fig. 3 show that the rate of thermal inactivation is independent of chain length since the rates are the same with acyl groups of 18 (Fig. 3A) and 16 (Fig. 3B) carbon atoms. It is known that under the conditions of these acyltransferase reactions all the unsaturated fatty acids tested are predominantly transferred to position 2 of glycerol-3-P whereas palmitate is transferred almost exclusively to position 1 (Table I). Thus the finding that enzyme activity is heat inactivated at the same rate when tested with all these acyl donors suggests that a single enzyme catalyzes acyl transfer to position 2 or to position 1 of glycerol-3-P. These results, coupled with the genetic evidence, indicate that the product of a single gene is involved in the specific acylation of glycerol-3-P to monoacylglycerol-3-P. This product may be either a single enzyme or a single protein or lipid essential to the activity of two or more acylating enzymes.

Further support for the proposal that a single enzyme catalyzes the acylation of glycerol-3-P was obtained by studying the chemical inactivation of an enzyme preparation derived from strain 8. Fig. 4 indicates the effect of treatment of the particles with increasing concentrations of maleic anhydride for 10 min. It is apparent that glycerol-3-P acyltransferase activity is severely inhibited by this treatment and that the decline of activity with increased concentration of inhibitor is the same whether oleyl-CoA or palmityl-CoA is used as acyl donor in the assay. Also shown in Fig. 4 is the effect of maleic anhydride treatment on 1-acylglycerol-3-P acyltransferase activity. It is noted that this activity, tested with either oleyl-CoA or palmityl-CoA is inhibited to a different extent than the glycerol-3-P acyltransferase.

Evidence that Acylation of Glycerol-3-P or of 1-Monoacylglycerol-3-P Involves Separate Enzymatic Activities—The maleylation experiment shown in Fig. 4 indicates that the enzyme or enzymes involved in the acylation of 1-acylglycerol-3-P is different from that which acylates glycerol-3-P. This is consistent with the differing pH and magnesium ion optima of the two activities (26). More rigorous evidence is presented in the
These experiments show that 1-acylglycerol-3-P acyltransferase has the same thermolability as that of their parent, strain 8. The 1-acylglycerol-P acyltransferase activity of these mutants CV2 and CV31 as shown in Fig. 6. The 1-acylglycerol-3-P acyltransferase activity of these mutants has the same thermolability as that of their parent, strain 8. These experiments show that 1-acylglycerol-3-P acyltransferase activity is no more thermolabile than the wild type enzyme in mutants which contain temperature-sensitive glycerol-3-P acyltransferase. Thus these experiments show that different enzymes catalyze acyl transfer to glycerol-3-P or to 1-acylglycerol-3-P. It should be noted that the rate of heat inactivation of 1-acylglycerol-3-P acyltransferase is the same with either palmitoyl-CoA or oleyl-CoA as a substrate.

It was of interest to determine whether the acyltransferase preparation in vitro could produce phosphatidic acid with a fatty acid distribution consistent with that found in the cellular phospholipids. A mixture of 1H-oleyl-CoA and 14C-palmitoyl-CoA was incubated with glycerol-3-P and the distribution of the fatty acids was determined in the isolated monoacylglycerol-3-P and phosphatidic acid fractions by scintillation counting. As seen in Table III, phosphatidic acid containing both fatty acids, monopalmitoylglycerol-3-P and monooleoylglycerol-3-P are all formed. Thus the system in vitro is able to produce phosphatidic acid of the required specificity.

DISCUSSION

The specificity of the system in vitro used in the study of the acylation of glycerol-3-P in this paper is remarkably consistent with the distribution of the fatty acid moieties of the phospholipids found in the bacterial cell (13, 45, 46). Palmitic acid is the predominant saturated fatty acid found in E. coli and it is found almost exclusively in the 1-acyl position of the cellular phospholipids. Myristic acid, the other major saturated fatty acid of E. coli, is found to be distributed about equally between positions 1 and 2 although position 2 predominates when an unsaturated fatty acid auxotroph is deprived of fatty acid (13). Stearic acid is only a trace component of E. coli phospholipids and the data in the literature suggest that it is randomly distributed between the two positions although the amounts have not been accurately quantitated. Palmitoleic and cis-vaccenic acids comprise the normal unsaturated fatty acid complement of E. coli and chiefly occupy position 2 of the cellular phospholipids. Oleic acid is not a normal component of E. coli (47) but can be efficiently incorporated when an unsaturated fatty acid auxotroph is supplemented with oleic acid (48). Under these conditions oleic acid is found exclusively in position 2 (13). The results presented strongly indicate that a single gene product is involved in the specific acylation of glycerol-3-P to monoacylglycerol-3-P. These reactions have been studied extensively in mammalian systems with little information as to the detailed enzymatic mechanisms involved in the specific acylation reactions. The present studies show that the acylation reactions might be rather simple in regard to the number of enzymes required. We have shown that the specific acylation of glycerol-3-P either requires only a single enzyme or is catalyzed by a number of enzymes sharing a common essential component. Further proof that a single enzyme catalyzes acyl transfer to positions 1 or 2 of glycerol-3-P must await protein solubilization and purification. However, if one protein catalyzes these reactions, then that protein must possess remarkable recognition abilities since it must catalyze palmitoyl transfer to position 1 or unsaturated acyl group transfer to position 2.

The complexity of the curves for the inactivation of 1-acylglycerol-3-P acyltransferase by maleylation is consistent with either of two possibilities. The curves can be explained if there are two enzymes which catalyze this reaction or if the completely maleylated enzyme retains about one-half the enzyme activity found in the untreated enzyme. If the former possi-

![Fig. 6. Comparative thermolabilities of the 1-acylglycerol-3-P acyltransferase activity of strain 8 and Mutants CV2 and CV31 as assayed with either palmitoyl-CoA (O--O) or oleyl-CoA (□--□) as a substrate. Typical specific activities of 1-acylglycerol-3-P acyltransferase of unheated samples of CV2 and CV31 are 5.9 and 4.9, respectively, with palmitoyl-CoA; 6.1 and 4.4, respectively, with oleyl-CoA (see Fig. 2 and "Materials and Methods" for experimental details).](image-url)
bility is correct, then the acylation of monoaoylglcerol 3-phosphate might be a complex process. The finding that 2-acylglycerol-3-P is produced in the acylation of glycerol-3-P suggests that this compound is an intermediate in phosphatidate synthesis. Experiments are now in progress to test if 2-acylglycerol-3-P is acylated and which, if any, of the presently described acyltransferase activities are involved in this acylation.

The experiments reported above indicate at least two enzyme activities, one catalyzing acylation of glycerol-3-P and the other acyltransferase activities are involved in this acylation.

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