Factors Affecting Muscle Glycogen Synthetase Activity

IV. COMPARATIVE STUDY OF THE DIFFERENT DEPENDENT FORMS OF GLYCOGEN SYNTHE-TASE*

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ENRIQUE BELLOCQPTOW, MARIA DEL CARMEN GARCIA FERNANDEZ,‡ LUTZ BIRNBAUMER,§ AND HÉCTOR N. TORRES¶

From the Instituto de Investigaciones Bioquímicas "Fundación Campomar" and Facultad de Ciencias Exactas y Naturales, Obligado 2490, Buenos Aires (98), R. Argentina

SUMMARY

The properties of the glucose 6-phosphate-dependent forms of glycogen synthetase obtained by incubation with calcium ions or with adenosine triphosphate were compared. The two preparations showed different sensitivity to the action of heat and trypsin. In addition, the synthetase obtained with adenosine triphosphate is reconvertible to the independent form while that prepared with Ca++ is not.

The possible physiological role of the two different mechanisms of formation of the glucose 6-phosphate-dependent forms of glycogen synthetase is discussed.

Krebs et al. found that the "nonactivated" phosphorylase b kinase can be transformed into the activated form by three different mechanisms: (a) by a transfer of phosphate from adenosine triphosphate to nonactivated phosphorylase b kinase (this reaction is accelerated by cyclic 3',5'-AMP (1)), (b) by a reaction in which Ca++ and a specific protein are involved, and (c) by treatment with trypsin (2).

Working with partially purified preparations of glycogen synthetase, it has been found that a transformation of the glucose-6-P-independent form to the dependent occurs under conditions similar to those mentioned for phosphorylase b kinase. The independent to dependent conversion in which ATP is a reactant is accelerated by cyclic 3',5'-AMP (3, 4). The reaction in which Ca++ is involved was studied and a specific protein factor was found to be required (5).

In this paper, experiments are reported which were designed to find out whether the different reactions in which glycogen synthetase is converted from independent to dependent have some common features and whether the enzymes formed can be distinguished from each other.

EXPERIMENTAL PROCEDURE

Materials—The reagents and chemicals used during this work were the same as in Paper II of this series (5). Crystalline trypsin (Tryptar) was a generous gift of Armour Laboratories (Buenos Aires). Soybean trypsin inhibitor was purchased from Sigma.

Analytical Methods—The radioactive samples were measured in a gas flow counter. Protein determinations were carried out by the method of Lowry et al. (6), and UDP according to Leloir and Goldemberg (7).

Assay of Glycogen Synthetase—All preparations to be assayed for glycogen synthetase were preincubated for 30 min at 30° in the presence of 50 mm mercaptoethanol (5). The composition of the standard reaction mixture was as follows: 5 μM UDP-glucose, 50 μM Tris-HCl buffer (pH 7.5), 2.5 μM EDTA, 1% glycogen, 10 mM glucose-6-P, if added, and enzyme in a total volume of 0.04 ml. The incubation was carried out for 30 min at 30°. The reaction was stopped by heating for 2 min at 100° and the UDP formed was measured by the method of Leloir and Goldemberg (7).

When UDP-[14C]-glucose was used, the radioactivity incorporated into glycogen was measured according to Leloir et al. (8). All assays were carried out both with and without 10 mM glucose-6-P.

Measurement of Michaelis constants was carried out with the standard reaction mixture as above, but with UDP-[14C]-glucose. In addition to this, in the case of the Km for glucose-6-P, the concentration of the latter was varied from 0 to 5 x 10⁻⁴ M, and in the determination of the Km for UDP-glucose, its concentration was varied from 0.045 to 1.62 x 10⁻⁴ M.

The ratio of independence of glycogen synthetase is expressed as follows: activity in the absence of glucose-6-P to activity in the presence of this hexose phosphate

\[
\frac{GS(D)}{GS(I)} = \frac{GS(I)}{GS(D)}
\]

where GS is glycogen synthetase, I is the independent form, and D is the dependent form.

Glycogen synthetase activity is expressed in the same units as in Paper II (5).
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Enzyme Preparations—Rats fed ad libitum and weighing from 150 to 250 g were transected at the level of the first lumbar vertebra, with a guillotine, while the animal was quiet. The operations which followed were carried out in the cold room between 0° and 4°. The muscle of the hind legs was used for the preparation of the acid precipitate fraction, at pH 5.2, as previously described (5). This extract was used directly in some experiments.

In a dialysis bag open at the top end, 1 volume of the acid precipitate fraction was mixed with 2 volumes of saturated ammonium sulfate solution containing 50 mM glycero-P-HCl buffer (pH 7.0), 4 mM EDTA, and 50 mM mercaptoethanol. Five minutes later, the bag was centrifuged inside a tube of a similar inner diameter, at 12,000 × g at 0°. The bag with the precipitate was drained and the supernatant fluid was discarded. Then the bag was knotted for dialysis without resuspending the pellet. The dialysis was carried out in three steps of 2 hours each, with two changes of the liquid. The first dialysis was made against 50 mM sodium glycero-P-HCl buffer (pH 7.0)-4 mM EDTA-50 mM mercaptoethanol, the second against 20 mM sodium glycero-P-HCl buffer (pH 7.0) 2 mM EDTA 90 mM mercaptoethanol, and the third against 10 mM sodium glycero-P-HCl buffer (pH 7.0)-1 mM EDTA-10 mM mercaptoethanol.

For the conversion reactions, 3 ml of the enzyme thus obtained were incubated with (a) 1 ml of 160 mM sodium glycero-P-HCl buffer, pH 7.2; (b) 1 ml of the same buffer containing 28 mM CaCl₂ and calcium-activating factor (5) in excess (the amount of the latter was ascertained by a previous assay); (c) 1 ml of 160 mM Tris-HCl buffer, pH 7.4, containing 7.2 mM ATP, 24 mM magnesium acetate, and 0.04 mM cyclic 3',5'-AMP; and (d) 1 ml of 160 mM sodium glycero-P-HCl buffer, pH 7.2, containing 0.2 mg of trypsin.

All incubations were carried out for 15 min at 30°.

EDTA (0.2 ml, 400 mM), pH 7.0, was added to the first three reactions, and 0.2 ml of 5 mg per ml of soybean trypsin inhibitor was added to the fourth. The samples were then dialyzed as described above. The enzymic preparations thus obtained were again adjusted to 4.2 ml with the buffer solution used for the third dialysis.

The enzyme prepared by the methods described above was called: (a) glycogen synthetase, independent form, control (GS(I)₀); (b) glycogen synthetase, dependent form, obtained with calcium (GS(D)ₙCa); (c) glycogen synthetase, dependent form, obtained with ATP-Mg⁺⁺-cyclic 3',5'-AMP (GS(D)ₙATP); and (d) glycogen synthetase, dependent form, obtained with trypsin (GS(D)ₙtryp).

Glycogen synthetase insensitive to the addition of calcium ions was prepared as described in Paper II of this series (5). Glycogen synthetase insensitive to the addition of ATP-Mg⁺⁺-cyclic 3',5'-AMP was prepared as follows: an acid precipitate fraction (150 ml, 10 mg of protein per ml) was applied to a column, 1.1 × 9 cm, of DEAE-cellulose previously equilibrated with 50 mM Tris-HCl buffer, pH 7.5, containing 1 mM EDTA. The column was eluted first with 800 ml of this buffer, and then an elution with 0.05 M sodium glycero-P-HCl buffer (pH 7.0)-4 mM EDTA-50 mM mercaptoethanol was performed, at a flow rate of 20 ml per hour. The fractions active at pH 7.0 were pooled, dialyzed, and the enzyme was further purified by dialysis against 50 mM Tris-HCl buffer, pH 7.5, containing 1 mM EDTA-4 mM NaF, and kept at 0°. Assays for glycogen synthetase activities were carried out in the absence and in the presence of 10 mM glucose-6-P. The starting ratio of independence of glucose synthetase was 0.27. The ratio of independence of glucose-6-P; •, glycogen synthetase, total activity.

**Table I**  
Independence of effects produced by Ca⁺⁺ and by ATP-Mg⁺⁺-cyclic 3',5'-AMP

<table>
<thead>
<tr>
<th>Experiment with</th>
<th>Additions</th>
<th>Ratio of independence</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ca⁺⁺-insensitive glycogen synthetase</td>
<td>H₂O</td>
<td>0.62</td>
</tr>
<tr>
<td></td>
<td>Ca⁺⁺</td>
<td>0.63</td>
</tr>
<tr>
<td></td>
<td>ATP-Mg⁺⁺-cyclic 3',5'-AMP</td>
<td>0.24</td>
</tr>
<tr>
<td>ATP-Mg⁺⁺-insensitive glycogen synthetase</td>
<td>H₂O</td>
<td>0.51</td>
</tr>
<tr>
<td></td>
<td>Ca⁺⁺-calcium-activating factor</td>
<td>0.30</td>
</tr>
<tr>
<td></td>
<td>ATP-Mg⁺⁺-cyclic 3',5'-AMP</td>
<td>0.52</td>
</tr>
</tbody>
</table>

* Calcium insensitive glycogen synthetase was prepared as indicated in the previous paper (5) and the ATP-Mg⁺⁺-insensitive one as described in text. The incubation mixtures contained: 50 mM sodium glycero-P, pH 7.3, and when indicated, 7 mM CaCl₂, 1.8 mM ATP, 6 mM magnesium acetate, and 0.01 mM cyclic 3',5'-AMP were added, in a final volume of 0.05 ml. In the experiment with ATP-Mg⁺⁺-insensitive glycogen synthetase, excess amounts of calcium-activating factor (5) were also added to the reaction mixture which contained Ca⁺⁺. The reaction mixtures were incubated for 6 min at 30° and then stopped by addition of 0.01 ml of 150 mM EDTA, pH 7.0, after which glycogen synthetase activities were measured as described under “Experimental Procedure.”

**Fig. 1.** Transformation of dependent glycogen synthetase to independent. An acid precipitate fraction was prepared as previously described (5) but the following modifications were made in order to obtain mainly dependent instead of independent glycogen synthetase. The skeletal muscle was homogenized with 4 mM EDTA containing 4 mM ethylene glycol bis(β-aminoethyl ether)-N,N,N',N'-tetraacetic acid, 4 mM sodium hydroxide, and 50 mM NaF. This homogenate was centrifuged at 3500 × g for 5 min. Then the supernatant fluid was brought to pH 5.2 with 1 M acetic acid and centrifuged at 5000 × g for 5 min. The acid precipitate thus obtained was resuspended into 20 mM Tris buffer containing 20 mM EDTA and 1 mM NaF and adjusted to pH 7.5. This preparation (0.1 ml) was incubated with 10 mM mercaptoethanol and 10 mM magnesium chloride, in a final volume of 0.114 ml. At the times indicated, aliquots were taken, mixed with standard substrate mixtures lacking UDP-glucose and with 10 mM NaF, and kept at 0°. Assays for glycogen synthetase activities were carried out in the absence and in the presence of 10 mM glucose-6-P. The reaction was started by addition of UDP-glucose. The starting ratio of independence of glycogen synthetase was 0.27. O, ratio of independence of glucose-6-P; •, glycogen synthetase, total activity.

† This method was carried out in collaboration with Dr. M. M. Appleman.
PREINCUBATION

INCUBATION

MINUTES

RATIO OF INDEPENDENCE

Fig. 2. Reversibility of the different dependent forms of glycogen synthetase. Glycogen synthetase was first preincubated with Ca++, ATP-Mg++-cyclic 3',5'-AMP, trypsin, or H2O as described under "Experimental Procedure." GS(I)H2O, GS(D)ATP, GS(D)C3, and GS(D)UP were then obtained by addition of 60 mM sodium glycero-P-HCl buffer (pH 7.5), 12.5 mM magnesium chloride, and 50 mM mercaptoethanol in a final volume of 0.04 ml. At the times indicated, 0.05 ml of 40 mM EDTA was added to the reaction mixture and glycogen synthetase activity was measured as described. O, GS(I)H2O; , GS(D)ATP; A, GS(D)C3; △, GS(D)UP.

with 3000 ml of the same solution but containing 100 mM NaCl. Then glycogen synthetase activity was eluted with 150 ml of the same buffer containing 330 mM NaCl. The activity was concentrated by means of a second DEAE-cellulose column as follows: the active fraction was diluted 3.5-fold with distilled water and applied to a column, 0.5 x 5 cm, equilibrated as the first one. The enzyme was eluted with Tris-HCl buffer, pH 7.5 (50 mM), containing 1 mM EDTA and 330 mM NaCl. The fractions having an absorbance at 280 nm higher than 1.0 were pooled and dialyzed against 50 mM Tris-HCl buffer, pH 7.5, containing 1 mM EDTA.

Ratios of independence of the different dependent forms of glycogen synthetase thus obtained varied between 0.15 and 0.25 and those of the independent forms between 0.50 and 0.70.

RESULTS

Comparison of Conversion Reactions Produced by Ca++ and ATP-Mg++-cyclic 3',5'-AMP—Evidence that the effect of Ca++ and that of ATP-Mg++-cyclic 3',5'-AMP are independent was obtained as follows.

As can be seen in Table I, the Ca++-insensitive enzyme responds to the addition of ATP-Mg++-cyclic 3',5'-AMP; conversely, an ATP Mg++-insensitive enzyme is transformed when Ca++ and calcium-activating factor are added.

Reversibility of Conversion Reaction Produced by ATP-Mg++ on Acid Precipitate Fraction—Traut (9) reported that the conversion of the independent form of glycogen synthetase to the dependent form by ATP-Mg++-cyclic 3',5'-AMP could be reversed by incubating the dependent form with glucose-6-P, Mg++, and reduced glutathione.

We have also observed that mercaptoethanol with Mg++ or with glucose-6-P, or the three compounds together, transforms the dependent to the independent form. As can be seen in Fig.

Fig. 3. Stability of glycogen synthetase at 42° after treatment with Ca++ or with ATP-Mg++-cyclic 3',5'-AMP. GS(I)H2O, GS(D)ATP, and GS(D)C3 were prepared as described under "Experimental Procedure" and treated at 42° for different times. At the times indicated, aliquots were taken, mixed with standard substrate mixture lacking UDP-glucose, and kept at 0°. Assays for glycogen synthetase activities were carried out in the presence of 10 mM glucose-6-P and the reaction was started by addition of UDP-glucose. Activities of untreated enzymes were taken as 100%.

Fig. 4. Stability of glycogen synthetase pretreated with Ca++ or with ATP-Mg++-cyclic 3',5'-AMP to the proteolytic action of trypsin. GS(I)H2O, GS(D)ATP, and GS(D)C3 were prepared as described under "Experimental Procedure." Mixtures containing enzyme, 100 mM sodium glycero-P-HCl buffer (pH 7.2), and 0.5 mg per ml of trypsin in a final volume of 0.05 ml were incubated at 30°. At the times indicated, 0.01 ml of 5 mg per ml of soybean trypsin inhibitor was added and glycogen synthetase activity was assayed in the presence of 10 mM glucose-6-P. O, GS(I)H2O; , GS(D)ATP; A, GS(D)C3; △, GS(D)TRP.
1, Mg$^{++}$ and mercaptoethanol produced an increase of the independent form with no major change in the total activity.

**Reversibility of Different Types of Dependent Forms of Glycogen Synthetase**—Reconversion of different types of the dependent form with mercaptoethanol and Mg$^{++}$ was tested. As shown in Fig. 2, while these compounds produce transformation of GS(D)$_{ATP}$, they have no effect either on GS(D)$_{cA}$ or on GS(D)$_{trp}$.

**Heat Resistance**—As shown in Fig. 3, GS(D)$_{cA}$ is the least stable, and is thus clearly different from GS(D)$_{ATP}$ and from GS(D)$_{trp}$.

**Proteolytic Action of Trypsin**—As can be seen in Fig. 4, GS(D)$_{cA}$ is also the most sensitive to the action of trypsin.

**pH Curves of Glycogen Synthetase Pretreated with Ca$^{++}$, ATP-**

![Fig. 5. Effect of pH on glycogen synthetase activity after treatment with Ca$^{++}$ or H$_2$O.](image1)

In incubation mixtures containing in a final volume of 0.04 ml: GS(I)$_{H_2O}$ or GS(D)$_{cA}$, 5 mM UDP-glucose, 2.5 mM EDTA, 1% glycogen, and 100 mM sodium glycero-P-HCl buffer (○) or Tris-HCl buffer (▲) of the indicated pH. The incubations were carried out in absence (■) and presence (□) of 10 mM glucose-6-P. After 30 min at 30°, the reaction was stopped by heating 1 min at 100°. Prior to UDP determination, Tris-HCl buffer of the adequate pH was added to the reaction mixture containing sodium glycero-P-HCl buffer in order to bring the final pH to about 7.5, and also, sodium glycero-P-HCl buffer was added to the reaction mixture containing Tris-HCl buffer to obtain the same final pH.

![Fig. 6. Effect of pH on glycogen synthetase activity after treatment with ATP-Mg$^{++}$ or trypsin.](image2)

The conditions were the same as in Fig. 5, but GS(D)$_{ATP}$ or GS(D)$_{trp}$ was used.

**Table II**

<table>
<thead>
<tr>
<th>Activity</th>
<th>$K_m$ for UDP-glucose</th>
<th>$V_{max}$ for UDP-glucose</th>
<th>$K_m$ for glucose-6-P</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Plus glucose-6-P</td>
<td>Minus glucose-6-P</td>
<td>Plus glucose-6-P</td>
</tr>
<tr>
<td>GS(D)$_{ATP}$</td>
<td>0.40 3.0</td>
<td>100 40</td>
<td>0.11</td>
</tr>
<tr>
<td>GS(D)$_{cA}$</td>
<td>0.66 2.5</td>
<td>100 20</td>
<td>0.9</td>
</tr>
<tr>
<td>GS(D)$_{trp}$</td>
<td>0.66 2.0</td>
<td>100 17</td>
<td>0.76</td>
</tr>
</tbody>
</table>

*The preparation of GS(D)$_{H_2O}$, GS(D)$_{ATP}$, GS(D)$_{cA}$, and GS(D)$_{trp}$ and measurement of the Michaelis constants were carried out as described under "Experimental Procedure."*

**Mg$^{++}$-Cyclic 3',5'-AMP and Trypsin**—As can be seen in Figs. 5 and 6, no major differences were obtained among the different dependent forms of glycogen synthetase preparations. Maximum activities in the presence of glucose-6-P oscillate around pH 8.2, and in the absence of the latter, around pH 7.5.

$K_m$ and Relative $V_{max}$ Values for UDP-Glucose and $K_m$ Values for glucose-6-P—In the experiment shown in Table II, the $K_m$ for UDP-glucose is higher in the absence of glucose-6-P. No major differences were observed among the different $K_m$ values corresponding to the several kinds of dependent forms.

**Effect of Ca$^{++}$ on the Four Different Forms of Glycogen Synthetase**—In order to see whether the calcium ions and ATP-Mg$^{++}$ act in the same region of the enzyme molecule, the different glycogen synthetase preparations were incubated with calcium. Fig. 7 shows that calcium acts on GS(D)$_{H_2O}$ and on GS(D)$_{ATP}$ in

![Fig. 7. Effect of Ca$^{++}$ on different glycogen synthetases.](image3)
a similar way, whereas it has little or no effect on the other two
glycogen synthetases. These results could be expected if the
action of ATP-Mg"-cyclic 3',5'-AMP and that of Ca++
are located on different points of the enzyme molecule.

Inhibition of Glucose and by UDP—Glucose, up to a concen-
tration of 100 μM, and 7.4 μM UDP, inhibits all the glycogen
synthetases by a factor of same order of magnitude. Glucose
diminishes the activity of glycogen synthetase by 50%, when
glucose-6-P is present, but gives no inhibition in the absence of
the phosphoric ester. UDP inhibits about 80%, when glucose-
6-P is present.

**DISCUSSION**

The transformation of the independent form of glycogen syn-
thetase to the dependent form produced by addition of ATP-
Mg" is stimulated by addition of cyclic 3',5'-AMP. The mechanism of action of this conversion consists in the phosphoryla-
tion of a serine residue, with a neighboring amino acid sequence
similar to the one found in the phosphorylation of phosphorylase
b (10).

The mechanism of the conversion of the independent form
into the dependent by Ca++ has not yet been solved. It could be
a proteolytic reaction, and the following indications would
agree with this hypothesis. (a) Dependent form of glycogen
catalytic activity formed by the action of trypsin is more similar to
that produced by Ca++-calcium-activating factor than that pro-
duced by ATP-Mg++, in reference to the reversibility by the
action of mercaptoethanol and Mg++. (b) The failure to obtain
in vitro conversion of GS(D)ca to the independent form with
EDTA and ethylene glycol bis(β-aminoethyl ether)-N,N'-tetra-
acetic acid would suggest that the GS(D)ca is not a calcium-
dependent enzyme complex. (c) Inactivation of calcium activating factor by the action of Ca++ has been noticed and it might be explained
by autolysis. A similar phenomenon was observed on the
protein factor acting on the activation of phosphorylase b kinase
by Ca++ (11). (d) In the process of coagulation there are stages in
which Ca++ activates protein factors with liberation of pep-
tides (12, 13).

However, Meyer (11) studied the proteolytic action of Ca++-
calcium-activating factor on substrates of known chemical struc-
ture and could not detect any effect. Therefore, if the action of
Ca++ on phosphorylase b kinase and glycogen synthetase is
proteolytic, it would be highly specific.

Another possibility would be the formation of a glycogen synthetase-calcium-activating factor-Ca++ complex similar to
that of actin-myosin-Ca++, which is formed during muscle con-
traction.

The independence of the effects of Ca++ and of ATP-Mg++ on
glycogen synthetase in vitro was proved when preparations of
glycogen synthetase, insensitive to the action of Ca++ and sensi-
tive to that of ATP-Mg++ (5), were obtained. On the other hand,
glycogen synthetase which is insensitive to the action of
ATP-Mg++ and sensitive to that of Ca++ (4) can also be pre-
pared.

A further indication of the independence of both effects was
obtained when the action of Ca++-calcium activating factor on the
different glycogen synthetases was studied. GS(D)ATP be-
comes more dependent by the action of Ca++-calcium-activating
factor. This effect would indicate different points of action of
both factors on the enzyme molecule.

Although the different forms of dependent glycogen synthetase
have some different properties they also have similar pH curves
and analogous Kₙ values for UDP-glucose and glucose-6-P, and
are equally inhibited by glucose and UDP. All these results
would support the hypothesis that the active center of these
forms is independent of glycogen synthetase and the places where
glucose-6-P acts are affected to the same degree by ATP (phos-
phorylation of a serine) and by Ca++ (separation of peptide or
formation of a complex with Ca++)

It was reported that epinephrine increases the levels of cyclic
3',5'-AMP (14), producing an increment of activated phos-
phorylase b kinase (15) and of dependent glycogen synthetase
(4) by accelerating the ATP Mg" action. In the muscular
contraction produced by electric excitation, an increase of the
active phosphorylase b kinase is observed, without change of
cyclic 3',5'-AMP concentration (16).

Since Ca++ acts as a trigger in muscular contraction (17), it is
possible that such contraction may be linked to the activation
of phosphorylase b kinase and to the conversion of independent
glycogen synthetase to dependent.

GS(D)ca is not reconvertible to the independent form in the
conditions under which GS(D)ATP is transformed. Moreover, GS(D)ca is more sensitive to the action of heat and trypsin and
less stable when stored at −20°.

Because of the properties of GS(D)ca and GS(D)ATP it is
tempting to identify the dependent form produced by epineph-
rine in vivo, with that obtained in vitro by ATP-Mg++-cyclic
3',5'-AMP, and the dependent form obtained by muscular con-
traction with that formed in vitro with Ca++.

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