# Effect of monensin on the Golgi apparatus of absorptive cells in the small intestine of the rat

## Morphological and cytochemical studies

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**Summary.** The effect of short-time treatment with the ionophore monensin, administered intraluminally at concentrations of 5 and 10 µM, was studied on the Golgi apparatus of absorptive cells in the small intestine of the rat. At 2–3 min after treatment most of the Golgi stacks exhibited dilated cisternae. At 4–5 min stacked cisternae were absent; they were replaced by groups of smooth-surfaced vacuoles. Dilatation and vacuolization occurred in the entire stacks without preferential effect on any particular Golgi subcompartment.

Monensin did not influence the cytochemical Golgi reaction of thiamine pyrophosphatase and acid phosphatase. The characteristic staining pattern of these two enzymes in all Golgi cisternae of absorptive cells in the proximal small intestine, and the reactivity restricted to trans cisternae in distal segments of the small intestine, were unchanged after treatment with monensin. In the distal small intestine, the cytochemical pattern allowed the monensin-induced vacuoles to be attributed to the former cis- or trans-Golgi face. Further, the cytochemical results demonstrate that vacuolization is not restricted to the stacked cisternae, but includes the trans-most cisterna. The latter, usually located at some distance from the Golgi stacks, has been defined as belonging to the GERL system in several types of cells. The clear response to monensin, an agent that selectively affects the Golgi apparatus, indicates common properties between trans-most and stacked Golgi cisternae.

**Key words:** Golgi apparatus – Monensin – Small intestine – Cytochemistry – Rat

The Golgi apparatus plays a central role in the intracellular traffic of membranes and of lysosomal and secretory materials (Tartakoff 1980; Farquhar and Palade 1981). Components of the Golgi complex are engaged in processing and packaging products destined to be transported to the cell surface and to lysosomes, and vice versa they are also the final destination for membranes retrieved from the plasma membrane (Farquhar 1982).

The carboxylic ionophore monensin, a metabolite of *Streptomyces cinnamonensis* (Pressman and Fahim 1982),

induces massive vacuolization of the Golgi apparatus accompanied by a perturbation of the intracellular traffic (Tartakoff and Vassalli 1977, 1978). In addition to a disturbance of endocytosis and recycling of cell surface receptors (Basu et al. 1981; Dickson et al. 1982; Marnell et al. 1982; Wilcox et al. 1982), monensin-induced inhibition of secretion has been described in several types of cells (Tartakoff and Vasalli 1977, 1978; Uchida et al. 1979; Ledger et al. 1980; Nishimoto et al. 1982). Specific functions of the Golgi apparatus, such as terminal glycosylation of glycoconjugates (Tartakoff and Vassalli 1979; Tartakoff et al. 1981; Niemann et al. 1982; Pesonen and Kääriäinen 1982; Ledger et al. 1983) and sulfatation (Kajiwara and Tanzer 1982) are impaired by treatment with monensin. Recent results on kidney cells from baby hamsters infected with Semliki forest virus (Griffiths et al. 1983; Quinn et al. 1983) point to a predominant effect of subcompartments located at the level of intermediate to trans cisternae.
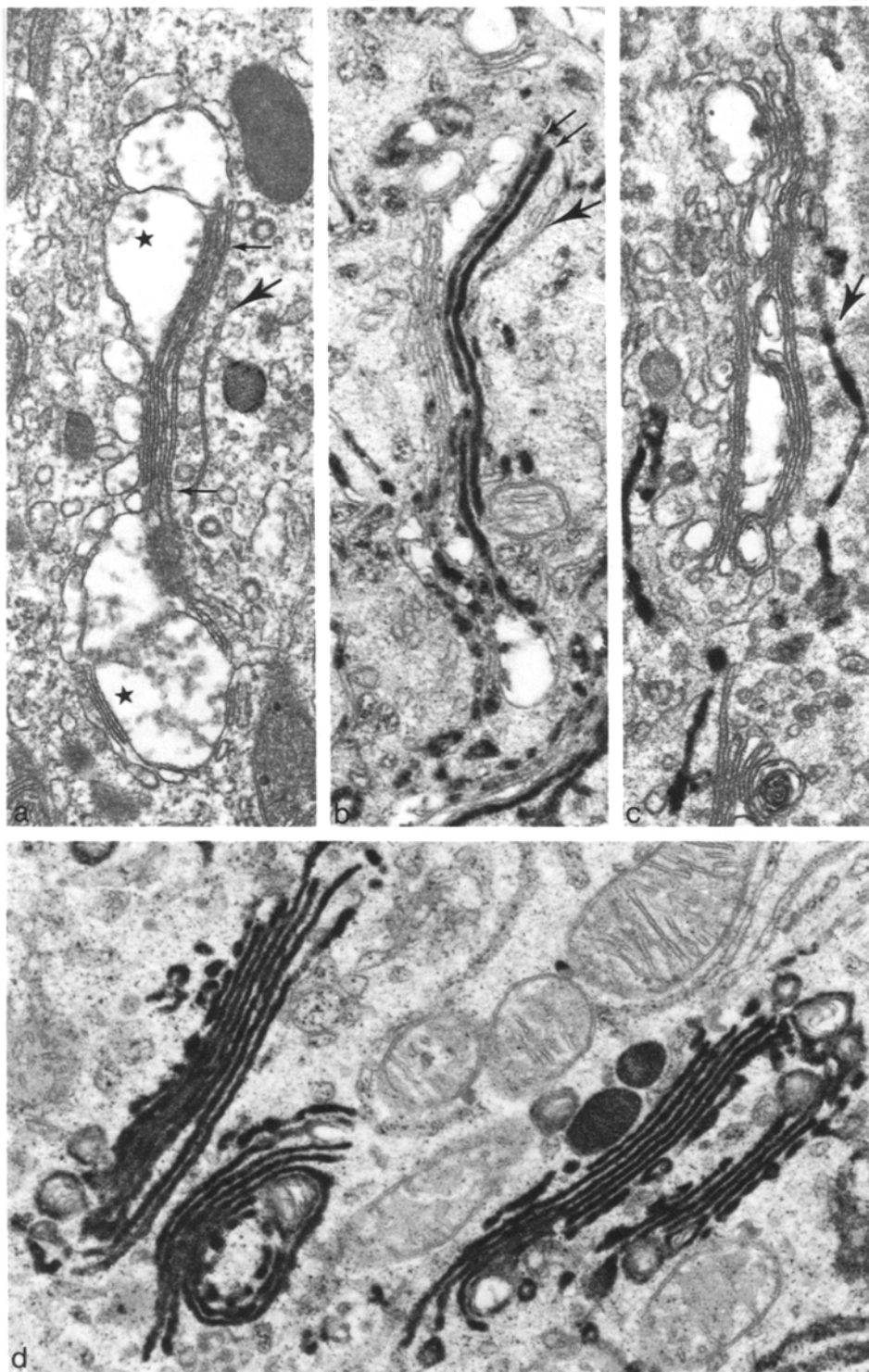
In most of the studies, which include morphological descriptions, monensin was administered at concentrations of 0.1–25 µM for 30 min and longer periods. Under these conditions stacked Golgi cisternae are lacking; instead, massive accumulations of large vacuoles dominate within the former Golgi areas.

We studied the effect of monensin, administered intraluminally at concentrations of 5 and 10 µM, on small-intestinal absorptive cells of the rat primarily under consideration of the following three aspects:

1. Are initial alterations after short periods of treatment (2–5 min) attributable to certain regions within the stacks? After longer periods of treatment, due to the loss of the polarity of the stacks, it is not possible to attribute vacuolized Golgi components to the former cis- or trans region.

2. It is open to discussion whether monensin may influence the cytochemical reaction of thiamine pyrophosphatase (TPPase) and acid phosphatase (AcPase), two enzymes widely used to characterize Golgi structures.

3. The role of the trans-most cisterna deserves special attention. It is not yet established whether this cisterna, frequently located at some distance to the stack, is a component of the Golgi apparatus (Hand 1980; Farquhar and Palade 1981; Broadwell and Oliver 1983; Pavelka and Ellinger 1983), or whether it belongs to the GERL-system and thus should be regarded as a separate entity (Golgi-associated endoplasmic reticulum/lysosomes; Novikoff 1976; Novikoff and Novikoff 1977). With respect to this question the response of the trans-most cisterna to monen-

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**Fig. 1 a–d.** Controls: Comparative structural (**a**) and cytochemical (**b–d**) demonstration of the organization of the Golgi stacks in absorptive cells of the small intestine.
**a** Duodenum: The clear polarity of this stack is representative for the entire length of the small intestine. Narrow cisternae at the trans side (→) contrast to dilated cisternae and vacuoles at the cis side containing lipid particles (★). The trans-most cisterna is located at some distance from the stack (➤). ×35000.
**b** TPPase – Distal jejunum: Two reactive cisternae (→) mark the trans side. The trans-most cisterna, setting off from the stack, reacts slightly (➤). × 45000.
**c** AcPase – Distal jejunum: Reaction is restricted to the trans-most cisterna, which resides at some distance to the stack (➤). ×45000.
**d** TPPase – Duodenum: Cis – as well as trans cisternae and vacuoles are highly reactive. ×35000

sin, known to affect the Golgi apparatus but not the endoplasmic reticulum (Tartakoff 1983), is of major significance.

## Materials and methods

Female albino rats (Sprague-Dawley), weighing 200–250 g, were fasted overnight. Laparatomy was performed under anaesthesia with pentothal, and ligatures were made in situ on segments of the duodenum, of the proximal or distal jejunum, or of the ileum, measuring approximately 6 cm in length. Subsequently, 0.3 ml of monensin[1] (Lilly Research Center Limited, Erl Wood Manor, England) at concentrations of 5 or 10 µM were injected into the lumen. After 2, 3, 4, or 5 min, respectively, the ligature was opened and monensin replaced by 2.5% glutaraldehyde (electron microscopy grade, Merck, Darmstadt), pH 7.2, buffered in

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1 Monensin was a generous gift of Dr. H. Kroeger, Lilly Research Centre Limited, Erl Wood Manor, Windlesham, Surrey, GU20 6PH England
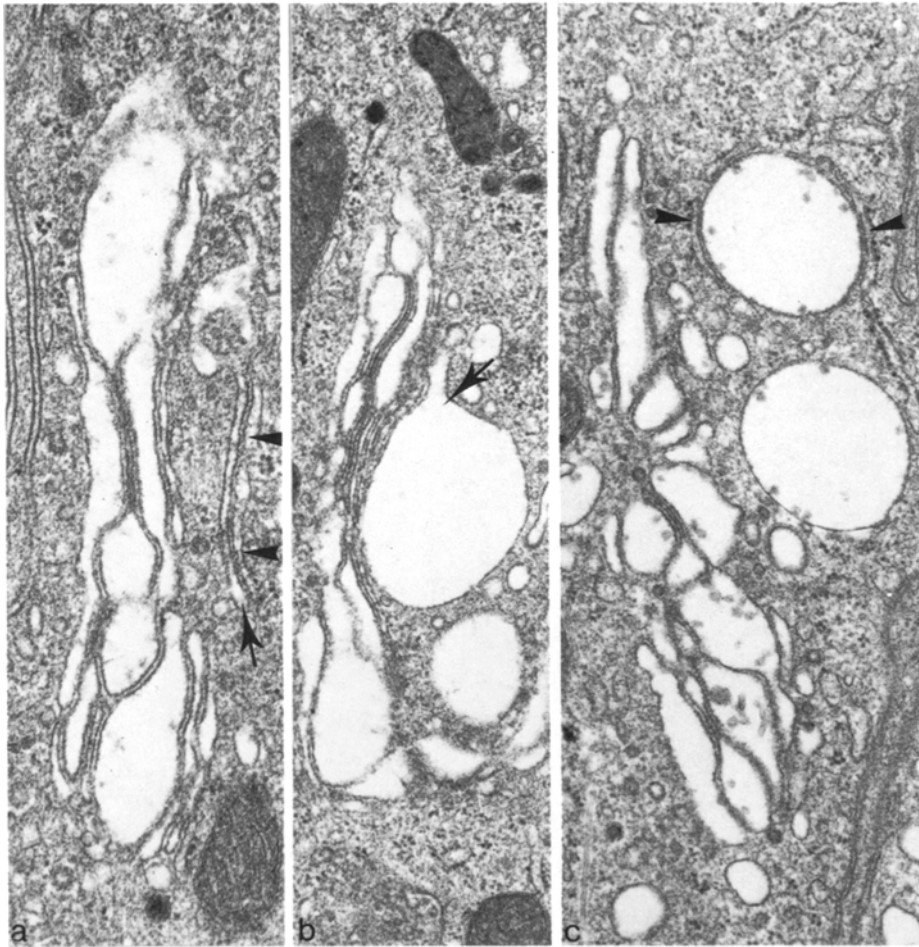
**Fig. 2.** Monensin, 2 min; **a–c** demonstrate moderately altered Golgi stacks, which predominate at 2–3 min after treatment with monensin. Irregular dilatations are apparent on the stacked cisternae.
**a** The trans-most cisterna, situated at some distance from the stack (→) and paralleled by endoplasmic reticulum (▶), is not affected. × 40000.
**b** Almost complete vacuolization characterizes the ultimate cisterna of one side (→). × 32000.
**c** Vacuoles located at some distance to the dilated cisternae accompany the stack. Being reactive for TPPase in absorptive cells of the proximal small intestine (see Fig. 4a) and for AcPase along the entire small intestine (see Figs. 4b, 5c), the vacuoles can be assumed to be derived from the trans-most cisternae. Endoplasmic reticulum closely adjacent to the vacuoles (▶) is excluded from vacuolization. × 32000

0.1 M cacodylate. Subsequently, small segments were excised and immersed in the same fixative.

For morphological studies fixation lasted for 2 h at 4° C. After an overnight rinse in buffer, specimens were postfixed in 1% veronal acetate-buffered $OsO_4$ dehydrated in a graded series of ethanol and embedded in Epon. For cytochemical studies, fixation was performed for 1 h, followed by an overnight rinse in 0.1 M cacodylate buffer containing 10% dimethylsulfoxide and 7.5% sucrose. 30–40 μm thick sections were cut on a freezing microtome.

TPPase activity was demonstrated according to the method of Novikoff and Goldfischer (1961); sections were incubated in a medium containing 25 mg thiamine pyrophosphate, 7 ml double-distilled water, 10 ml Tris maleate buffer, pH 7.2, 5 ml 0.025 M manganese chloride, 3 ml 1% lead nitrate, and 1.25% sucrose for 70 min at 37° C.

For localization of AcPase according to the method of Barka (1964) sections were incubated at pH 5.0 in a medium containing 10 ml 1.15% sodium β-glycerophosphate, 10 ml Tris-maleate buffer, pH 5.0, 10 ml double-distilled water, 20 ml 0.2% lead nitrate, and 7.5% sucrose for 20 min at 37° C.

For cytochemical controls equivalent media lacking the substrate were used.

Postfixation, dehydration and embedding were performed as described above. Ultrathin sections either unstained or stained with alcoholic uranyl acetate and alkaline lead citrate were examined in a Philips EM 400 electron microscope.

## Results

### Controls

Golgi stacks of mature small intestinal absorptive cells mostly display a clear polarity (Fig. 1a): dilated cisternae containing lipid particles characterize the cis side; at the trans side narrow cisternae predominate. The trans-most cisterna frequently is situated at some distance to the stack.

Unlike the morphological appearance of the Golgi stacks, which is constant along the entire length of the small intestine, the cytochemical reaction pattern of TPPase and AcPase differs between proximal and distal small intestinal segments (Pavelka and Ellinger 1982; Fig. 1b–d). In the duodenum and in the proximal jejunum all cisternae are strongly reactive for both enzymes (Fig. 1d). The intensity of the reaction declines gradually from proximal to distal small intestinal regions. In the distal jejunum and in the ileum TPPase and AcPase are restricted to cisternae of the trans side: TPPase is apparent over one to three trans cisternae; the trans-most cisterna stains slightly for TPPase or is free of reaction (Fig. 1b) but exhibits high AcPase activity (Fig. 1c).

In addition to the staining of the Golgi apparatus, primary and secondary lysosomes are reactive for TPPase and AcPase. In accordance with former reports (Saito and Ogawa 1966; Hugon et al. 1970; Goldfischer et al. 1971; Novikoff and Novikoff 1977) slight reaction for TPPase is demonstrable in the endoplasmic reticulum and at the apical and lateral plasma membrane.
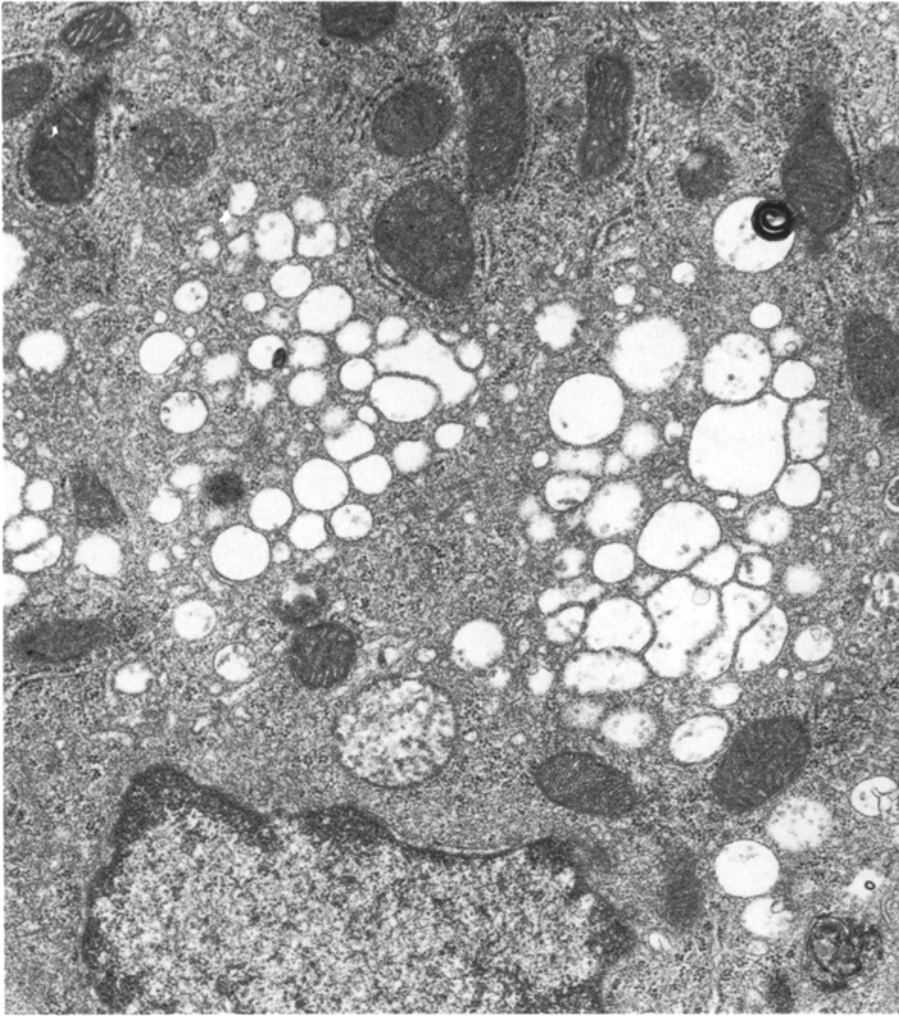
**Fig. 3.** Monensin, 5 min. In the supranuclear area groups of vacuoles characterize the former Golgi region. Stacked cisternae are not demonstrable. Nuclear envelope and endoplasmic reticulum are unaffected by the monensin-induced vacuolization. ×25000
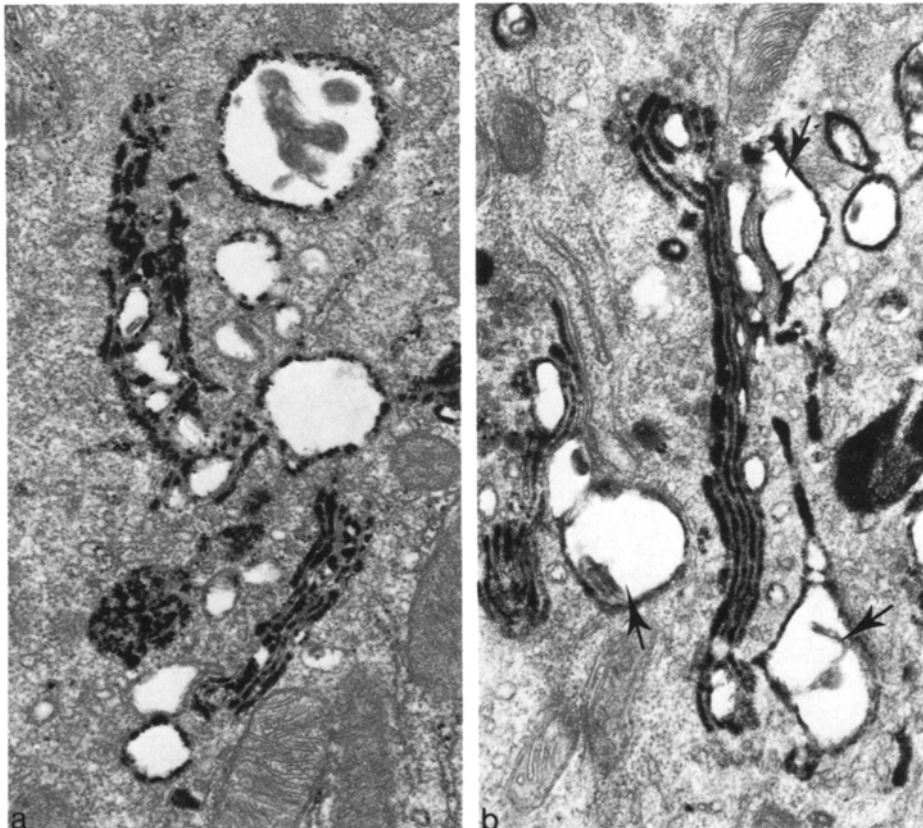


**Fig. 4a, b.** Monensin, 2 min, duodenum. **a** TPPase; **b** AcPase. Stacked cisternae as well as accompanying vacuoles are strongly reactive for both enzymes. Slight dilatations are apparent on individual cisternal segments. In (**b**) the trans-most cisterna exhibits conversion into vacuoles (→). **a** ×45000; **b** ×40000
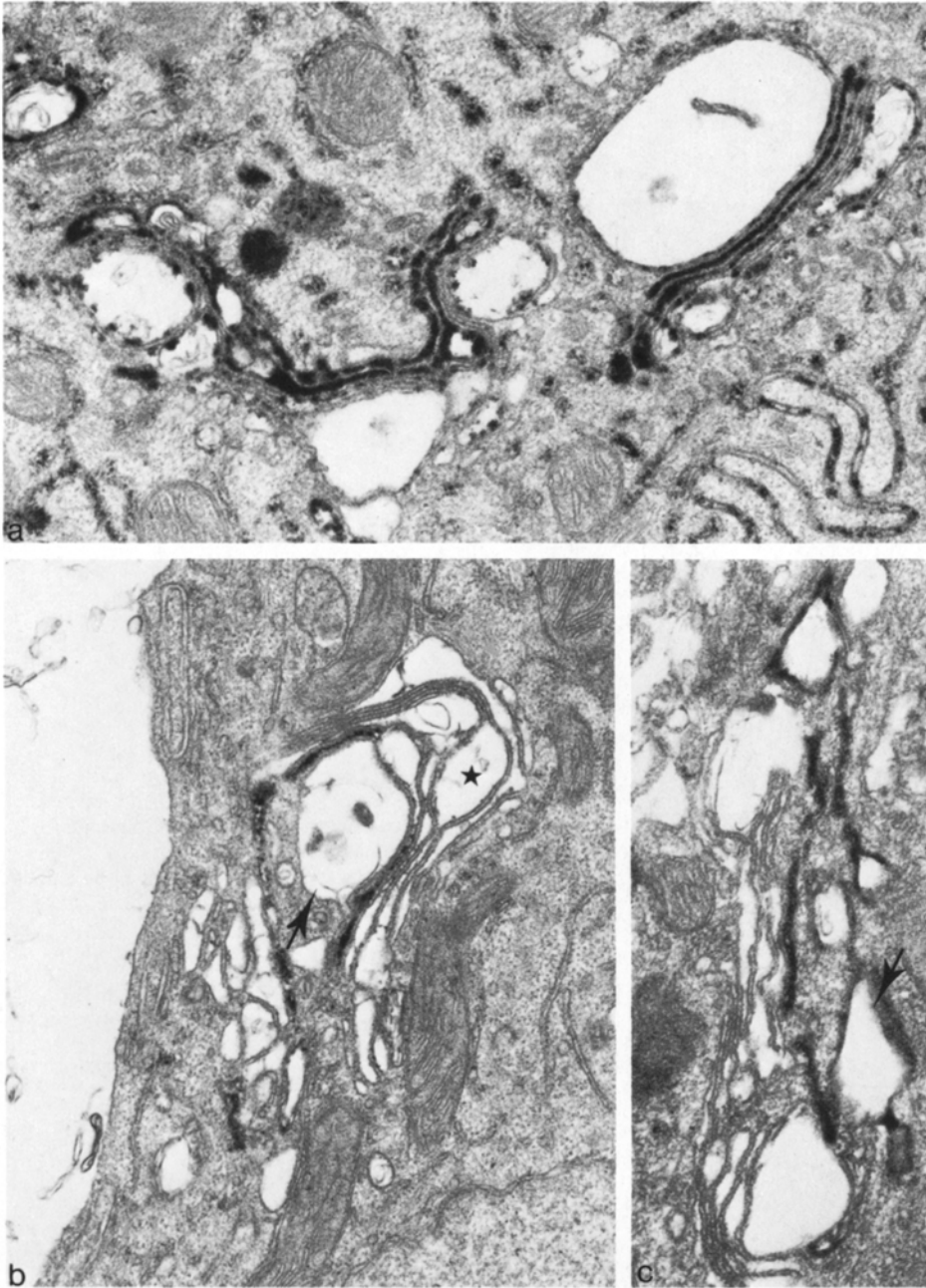
Fig. 5a–c. Monensin, 2 min, distal small intestine.
a TPPase, distal jejunum. Intense reaction of two cisternae at the trans aspect of the stacks. Proximal and trans-most cisternae exhibit traces of reaction product. At the left stack cis cisternae are vacuolized, whereas vacuolization of the trans-most cisterna is apparent on the right stack. × 37000.
b TPPase, ileum. Reaction is restricted to one cisterna at the trans side of the stack. Cis cisternae (★) as well as trans-most cisterna (➤) are devoid of reaction product. × 37000.
c AcPase, distal jejunum. At the trans aspect of the stack two cisternae exhibit reaction product. The trans-most cisterna (➤) partially is converted into vacuoles. × 40000

## Monensin-treated animals

*Ultrastructure.* 2–5 min after administration of monensin most Golgi stacks of the absorptive cells along the upper third of the villi are affected. The degree of the alterations depends on the duration of treatment. Golgi cisternae may either be irregularly dilated, or may be replaced by smooth-surfaced vacuoles. The nuclear envelope and the endoplasmic reticulum remain unaffected.

a) At 2–3 min after treatment with monensin slightly altered stacks predominate. In rare cases the stacked cisternae are dilated, whereas the trans-most "setting-off cisterna" is unaffected (Fig. 2a). The majority of the stacks, however, exhibits the trans-most cisterna in a vacuolized form (Fig. 2b) and the stacked cisternae dilated but not converted into vacuoles. Vacuolization of the trans-most cisterna appears to precede vacuolization of the stacks.

A clear attribution of initial dilatation to certain regions within the stacks is not possible. Dilatation widely occurs on all cisternae throughout the stacks, thus resulting in a loss of the polarity (Fig. 2c). Morphologically, cis- and trans sides cannot be distinguished in these cases. The vacuoles, which accompany the stacks at some distance, are reactive for AcPase (see below) and thus can be assumed to be derived from the trans-most cisternae; they are helpful in the definition of the trans side on these stacks.

Transitional elements of the endoplasmic reticulum residing closely adjacent to the vacuoles are excluded from vacuolization (Fig. 2c).

b) Treatment for 4–5 min causes massive vacuolization of the Golgi apparatus (Fig. 3). Stacks of flattened cisternae are not demonstrable; vacuoles are restricted to the Golgi area. Morphologically, it is impossible to decide which of the vacuoles are derived from the cis- or trans side.
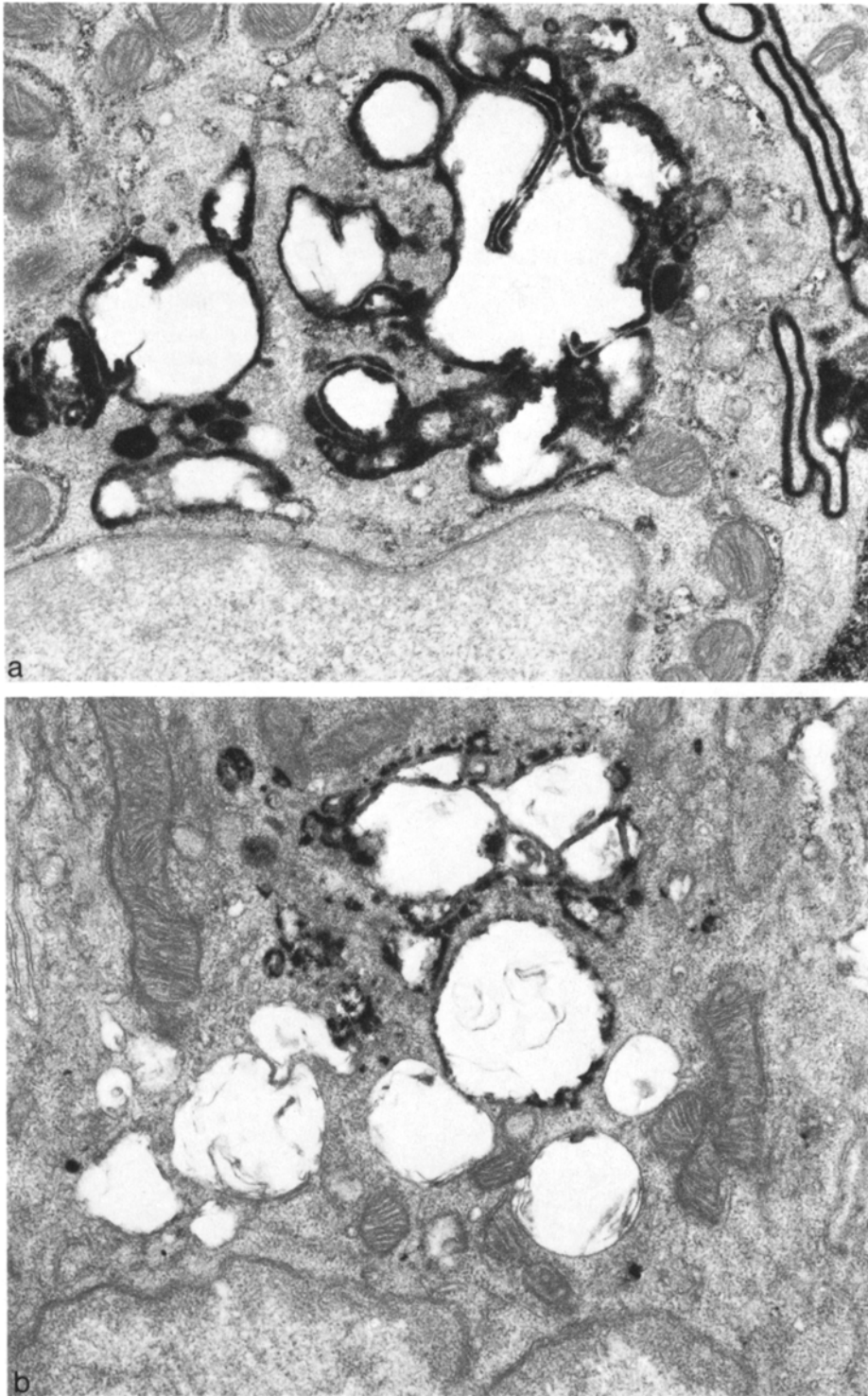
Fig. 6a, b. Monensin, 5 min.
a TPPase, duodenum. All of the vacuoles that occupy the former Golgi region are highly reactive. ×30000.
b AcPase, distal jejunum. Reaction is restricted to some of the monensin-induced vacuoles; others are devoid of reaction. ×26000

*Cytochemistry.* Monensin applied for 2–5 min does not affect, or only minimally alters the activity of TPPase and AcPase, as far as can be demonstrated cytochemically. The Golgi reaction in absorptive cells of treated animals reflects that of controls.

a) At 2–3 min of treatment in the absorptive cells of the duodenum and proximal jejunum all stacked cisternae as well as the trans-most cisterna, independent from the degree of vacuolization, react intensely for TPPase (Fig. 4a) and AcPase (Fig. 4b). In absorptive cells of the distal jeju-

num and of the ileum strong TPPase activity is apparent over 1–3 cisternae at the trans aspect of the stacks (Fig. 5a, b). The irregularly dilated cisternae of the cis side, and the vacuolized trans-most cisternae show slight reaction in the disital jejunum (Fig. 5a), and are devoid of reaction product in the ileum (Fig. 5b). Strong AcPase activity is demonstrable over the vacuolized trans-most cisternae (Fig. 5c), and may in addition be apparent over 1–2 cisternae at the trans side of the stacks.

b) At 4–5 min of treatment, in absorptive cells of the

proximal small intestine, all of the vacuoles that occupy the former Golgi area are highly reactive for TPPase (Fig. 6a) and AcPase. In contrast, in absorptive cells of the distal small intestine, the reaction for these enzymes is restricted to a portion of the vacuoles (Fig. 6b).

## Discussion

In the present study we analyzed, in the absorptive cells of the small intestine of the rat, the response of the Golgi apparatus to short-time treatment with the ionophore monensin. Intraluminal application at concentrations of 5 and 10 µM causes dilatation and vacuolization of all Golgi cisternae. The cytochemical reaction of TPPase and AcPase in absorptive cells of treated animals mirrors that of controls.

Vacuolization of the Golgi apparatus induced by monensin is a constant morphological finding (for review, see Tartakoff 1983). In ganglion cells, preferential dilatation of intermediate cisternae has been reported (Lindsey and Ellisman 1981); in contrast, uniform vacuolization of all cisternae throughout the stacks has been shown in a multiplicity of cell types treated with monensin at concentrations of 0.1–25 µM for 30 min and longer periods (Tartakoff and Vassalli 1977, 1978; Ledger et al. 1980; Tartakoff et al. 1981; Nieman et al. 1982; Griffiths et al. 1983; Quinn et al. 1983; Tougard et al. 1983). In agreement with the long-term studies, our results obtained at 2–5 min after treatment revealed uniform response of all cisternae constituting the stacks; we were unable to demonstrate a preferential effect on any particular Golgi sub-compartment. This disagrees with the results gained from functional studies on other types of cells (Tartakoff et al. 1981; Nieman et al. 1982; Griffiths et al. 1983; Quinn et al. 1983), pointing to a disturbance at the level of intermediate to trans Golgi regions. It is not yet clear whether or not a correlation exists between the monensin-induced impairments of the Golgi function and the morphologically demonstrable vacuolization.

In addition, we did not find an increase in the number of stacked cisternae that has been observed to precede the gross vacuolization of Golgi components in embryonic carrot cells (Morré et al. 1983).

The uniform response of stacked cisternae to monensin results in a loss of the polarity of the stacks. For further characterization of the dilated and vacuolized Golgi stacks the cytochemical pattern is essential. Consistent with the results obtained with other types of cells (Griffiths et al. 1983; Tougard et al. 1983) monensin does not influence the Golgi reaction of TPPase and AcPase. Different staining patterns of these enzymes are found in absorptive cells of the duodenum, jejunum, and ileum (Pavelka and Ellinger 1982; Ellinger and Pavelka 1982); they may reflect functional differences between the proximal and distal small intestine. The characteristic reaction of TPPase and AcPase in all Golgi cisternae in the proximal portion of the small intestine, and the reaction restricted to trans cisternae in distal segments, remain unchanged after treatment with monensin. In absorptive cells of the distal small intestine, because of the polar distribution of the reaction product within the stacks, and the localization of TPPase and AcPase, aids in defining cis- and trans sides on the vacuolized stacks. By means of the AcPase reaction, the vacuoles located at some distance to the stacks can be characterized as derivates of the trans-most cisternae. The cytochemical

results demonstrate that the monensin-induced vacuolization is not restricted to the stacked cisternae but includes the trans-most "setting – off cisterna". Vacuolization of the trans-most cisterna appears even to precede dilatation of the stacked cisternae. In this respect, our results contrast to those gained from GH3-prolactin cells (Tougard et al. 1983), which indicated a fragmentation rather than vacuolization of the trans-most cisterna.

The relationship of the trans-most cisterna either to the Golgi apparatus or to the endoplasmic reticulum is not yet established (Hand 1980; Farquhar and Palade 1981; Broadwell and Oliver 1983; Pavelka and Ellinger 1983). In a multiplicity of cell types, the trans-most cisterna of Golgi stacks has been defined as "GERL" (Golgi-associated endoplasmic reticulum/lysosomes; see Novikoff 1976; Novikoff and Novikoff 1977), and thus, suggested to represent a specialized region of the endoplasmic reticulum. The clear response to monensin, an agent that affects the Golgi apparatus but not the endoplasmic reticulum (Figs. 2c, 3–6; Tartakoff 1983), indicates common properties between trans-most and stacked cisternae, and suggests a relationship of the trans-most cisterna to the Golgi apparatus rather than to the endoplasmic reticulum.

In absorptive cells of the small intestine, transitional elements of the endoplasmic reticulum are frequently located closely adjacent to trans Golgi cisternae (Pavelka and Ellinger 1983). The significance of this association is not clear; it is notheworthy, however, that the "Golgi-associated endoplasmic reticulum" retains its position despite the massive vacuolization of the trans-most cisternae, but is not included in the monensin-induced disorganization of the Golgi apparatus.

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