HIGH K⁺,Na⁺-DEFICIENT SOLUTION INHIBITS TENSION, O₂ CONSUMPTION, AND ATP SYNTHESIS IN SMOOTH MUSCLE

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Abstract—In guinea pig taenia coli, added 45.4 mM K⁺ induced a sustained contraction, increased the rate of oxygen consumption, and slightly decreased the ATP content. In substituted 154.2 mM K⁺, Na⁺-deficient solution, only a transient contraction was induced. Oxygen consumption also showed only a transient increase and ATP content of the muscle rapidly decreased. Such an inhibition of sustained contraction and the decrease in both oxygen consumption and ATP content were recovered when 5.5 mM pyruvate or 50 mM NaCl was added during the 154.2 mM K⁺-induced contraction. In rabbit aorta, substituted 80 mM K⁺, 74.2 mM Na⁺ solution induced a sustained contraction, increase in oxygen consumption, and no change in ATP content. The 80 mM K⁺ solution without added glucose also induced a sustained contraction followed by a slight increase in oxygen consumption and a slight decrease in ATP content. The 154.2 mM K⁺, Na⁺-deficient solution produced similar changes in both oxygen consumption and ATP content as the 80 mM K⁺, glucose depleted solution. However, the 154.2 mM K⁺ solution induced only a transient contraction in the vascular smooth muscle. When 100 mM sucrose was hyperosmotically added to the 154.2 mM K⁺ solution, the suppressed muscle tension increased again, although the ATP content did not increase. From these and the previous results, it is concluded that glucose utilization by the taenia coli is inhibited in the 154.2 mM K⁺, Na⁺-deficient solution, and the decreased energy production of the muscle cell does not compensate the increased energy consumption induced by the high concentration of K⁺. In the aorta, although the Na⁺-deficient solution also decreases ATP production, it is the cell swelling induced by a high KCl concentration in the medium, not the decrease in energy metabolism, that has a direct inhibitory effect on muscle tension.

High concentration of K⁺ is frequently used to investigate the excitation-contraction coupling in smooth muscle. High K⁺ is usually applied either by replacing Na⁺ with K⁺ or by adding K⁺ salts to a physiological solution (1).

In the intestinal smooth muscle of guinea pig taenia coli, hypertonicity added K⁺ induced a sustained contraction, while substituted K⁺, Na⁺-deficient solution induced only a transient contraction (2, 3). Similar changes
were also reported in rabbit aorta (4). Suzuki et al. (5) found in taenia coli that addition of NaCl or pyruvate maintained the sustained tension in the substituted K⁺, Na⁺-deficient solution and suggested that Na⁺-deficiency might inhibit the glucose utilization of the smooth muscle and thus inhibits the sustained contraction. On the other hand, addition of sucrose to the substituted K⁺ solution to prevent the swelling of the muscle cell (6) also prevented the decrease in sustained contraction in the aorta (4). In the present experiments, we examined the changes in energy metabolism of the taenia coli and aorta in added K⁺ and substituted K⁺,Na⁺-deficient solutions.

MATERIALS AND METHODS

Taenia coli strips were dissected from the caecum of male guinea pigs weighing 250 to 300 g. Muscle strips of approximately 20 mm long, 50 mm long, or 7 mm long were used for tension, oxygen consumption, or ATP determination respectively. Helical strips (3–4 mm wide) of thoracic aorta removed from male New Zealand White rabbits weighing 2.0 to 2.5 Kg, were made as described by Furchgott (7). The adventitial layer was separated from the media-intimal layer by the method of Karaki and Urakawa (8) and approximately 10 mm long, 50 mm long, or 5 mm long strips were made for tension experiments, oxygen consumption, or ATP determination, respectively.

Since the treatments of the muscle with various high K⁺ solutions change the muscle wet weight (4, 5), muscle strips were weighed before the initiation of the experimental procedures. All the values including ATP content and oxygen consumption were expressed in terms of this initial tissue wet weight. Then, the muscle strips were attached to the holders under a resting tension of 0.2 to 0.5 g for taenia coli and 1.0 g for aorta and equilibrated for 60 min in normal physiological solution with the following composition (mM): NaCl, 136.9; KCl, 5.4; CaCl₂, 2.5; MgCl₂, 1.0; NaHCO₃, 11.9; and glucose, 5.5. The solution was continuously bubbled with a mixture of 95% O₂ and 5% CO₂ at 37°C and pH 7.2. Hypertonically added 25.4 mM or 45.4 mM K⁺ solution was made by increasing the KCl concentration in the above solution to 25.4 mM and 45.4 mM, respectively. Substituted 80 mM K⁺, 74.2 mM Na⁺ solution or 154.2 mM K⁺, 0 mM Na⁺ solution was made by substituting an appropriate amount of Na⁺ with equimolar K⁺ in the above solution.

Isometric contraction of the muscle was recorded with a force displacement transducer connected to a polygraph (Nihon Kohden, Japan). O₂ consumption was measured by a similar method as described earlier (9–11) using a Clark-type oxygen electrode (Rank Brothers, UK). Adenosine triphosphate (ATP) content was determined by the method described by Strehler and McElroy (12) using the Lumac Biometer M 1030 or M 2010 (Lumac B V, Netherlands). The weight of each of the muscle strips used for the ATP determination was 5–10 mg. Statistical significance was determined by the Student's t-test.

RESULTS

Changes in the rate of oxygen consumption in the taenia coli are shown in Table 1. The resting O₂ consumption was 0.618 μmol/g/min. The application of 45.4 mM K⁺ induced a maximum sustained contraction averaging 2.1±0.1 (n=30) Kg force/cm² and also increased the rate of O₂ consumption to 1.236 μmol/g/min. When 25.4 mM K⁺ was added to induce half a maximum contraction, O₂ consumption also increased to approximately half the increment induced by 45.4 mM K⁺. Substituted 154.2 mM K⁺ induced a transient contraction followed by a small sustained contraction; and at 20 min
Table 1. Changes in the rate of oxygen consumption and the muscle tension in guinea pig taenia coli

| Condition                      | Rate of oxygen consumption µmol/g/min±S.E. | N | % change | Muscle tension Kg force/cm² |
|-------------------------------|------------------------------------------|---|----------|----------------------------|
| Control                       | 0.618±0.033                              | 18 | 0        | 0                          |
| 25.4 mM K⁺ (20 min)           | 0.942±0.063                              | 8  | +52      | 1.1                        |
| 45.4 mM K⁺ (20 min)           | 1.236±0.072                              | 10 | +100     | 2.1                        |
| 154.2 mM K⁺ (20 min)          | 0.732±0.030                              | 10 | +18       | 0.4                        |
| 154.2 mM K⁺ (60 min)          | 0.579±0.090                              | 5  | N.S.     | 0.2                        |
| 154.2 mM K⁺+5.5 mM pyruvate (80 min) | 1.092±0.078                      | 5  | +78       | 1.2                        |
| 154.2 mM K⁺+50 mM NaCl (80 min) | 1.116±0.072                      | 5  | +81       | 1.4*                      |
| 154.2 mM K⁺+10⁻⁴ M ouabain (60 min) | 0.531±0.060                        | 10 | N.S.     | 0.2                        |
| 154.2 mM K⁺+10⁻⁴ M ouabain+5.5 mM pyruvate (80 min) | 0.876±0.033                  | 5  | +42       | 1.8                        |
| 154.2 mM K⁺+10⁻⁴ M ouabain+50 mM NaCl (80 min) | 0.930±0.114                      | 5  | +50       | 0.7**                     |
| 154.2 mM K⁺+glucose removal (60 min) | 0.531±0.084                    | 5  | N.S.     | 0                          |
| 154.2 mM K⁺+glucose removal+50 mM NaCl (80 min) | 0.327±0.081                  | 5  | +47       | 0                          |

All the values were obtained after the incubation period indicated in the parenthesis. Pyruvate or NaCl was added 60 min after the application of 154.2 mM K⁺ as shown in Fig. 1. Ouabain was added 30 min after, and glucose was removed simultaneously with the application of 154.2 mM K⁺. N: number of experiments for the oxygen consumption. Muscle tension is the mean of at least 6 muscle strips, and the S.E. value (less than 5% of the respective mean value) is not shown in the table. N.S.: not significantly different (P<0.05) from the control value. *Measured at 60 min after the application of NaCl when muscle tension reached a steady level as shown in Fig. 1. **Peak tension of the transient increase measured approximately 20 min after the application of NaCl.

and 60 min after the application of 154.2 mM K⁺, only 21.3±1.4% (n=6) and 10.6±2.5% (n=6) of the maximum contractile tension, respectively, remained (Fig. 1). Oxygen consumption measured 20 min after the application of 154.2 mM K⁺ was only 0.114 µmol/g/min higher than the control level, and no increase was detected after 60 min (Table 1). Pyruvate (5.5 mM) or 50 mM NaCl, added 60 min after the application of the 154.2 mM K⁺, gradually increased the muscle tone reaching 57.3±2.6% (n=6) or 67.0±3.4% (n=6), respectively, of the maximum contraction (Fig. 1). Oxygen consumption was also increased by the addition of pyruvate or NaCl to the level comparable to the increase in muscle tone. Ouabain, 10⁻⁴ M, did not abolish the increase in O₂ consumption induced either by pyruvate or by NaCl. The increase in muscle tone induced by pyruvate was also not affected by ouabain. The increase in muscle tone induced by NaCl was transient in the presence of ouabain, possibly because excess accumulation of Na⁺ in the cell inhibits excitation-contraction coupling in the taenia coli (13). On the other hand, when glucose was removed from the medium, the effects of added NaCl on both muscle tone and oxygen consumption were abolished as shown in the Table 1. From these data, the correlation between the rate of oxygen consumption and the muscle tension was described as follows:

Rate of O₂ consumption (µmol/g/min) = 0.33 x muscle tension (Kg force/cm²) + 0.539 (n=12, r=0.883)

Therefore, taenia coli seemed to consume 0.33 µmol O₂/g tissue/min to maintain 1 Kg
force/cm² during high-K⁺ induced sustained contraction.

In Fig. 1, changes in muscle tension and ATP content in the taenia coli are summarized. ATP content in the resting muscle was 1.98±0.03 umol/g (n=30). In the presence of 45.4 mM K⁺, ATP content slightly decreased; and 120 min after the application of K⁺, ATP content was 1.67±0.06 umol/g (n=24). Substituted 154.2 mM K⁺ more rapidly decreased the ATP content to 1.58±0.06 umol/g (n=12) and to 1.23±0.06 umol/g (n=24) at 60 min and 120 min after the application of K⁺, respectively. When 5.5 mM pyruvate or 50 mM NaCl was added 60 min after the application of 154.2 mM K⁺, ATP content increased to a level similar to that in the presence of 45.4 mM K⁺.

Changes in the rate of oxygen consumption and muscle tension in rabbit aorta are shown in Table 2, and the changes in ATP content are shown in Table 3. In normal solution, the muscle consumed 0.076 umol O₂/g/min and contained 0.70 umol ATP/g. Application of 80 mM K⁺ induced a sustained contraction of nearly maximum level, and ATP content was not affected by 80 mM K⁺. On the other hand, the muscle contraction induced by 154.2 mM K⁺ gradually decreased; and 120 min after the application of K⁺, only 40.3±3.2% (n=8) of the maximum contraction remained. The rate of oxygen consumption was higher (42%), and the ATP content was lower (-27%) than the respective control levels at the 120th min of the application of 154.2 mM K⁺. When 100 mM sucrose was added to the 154.2 mM K⁺ solution, the decrease in the sustained contraction was prevented (93.5±4.4%; n=6), as has been reported (4). The addition of sucrose,

![Graph](image)

**Table 2.** Changes in the rate of oxygen consumption and muscle tension in rabbit aorta

| Condition         | Rate of oxygen consumption (µmol/g/min±S.E.) | % change | Muscle tension (Kg force/cm²) |
|-------------------|--------------------------------------------|----------|-------------------------------|
| Control           | 0.076±0.007                                 | 0        | 0                             |
| 80 mM K⁺ (20 min) | 0.211±0.005                                 | +177     | 0.81                          |
| 80 mM K⁺ (120 min)| 0.196±0.008                                 | +156     | 0.82                          |
| 154.2 mM K⁺ (20 min)| 0.216±0.007                               | +183     | 0.80                          |
| 154.2 mM K⁺ (120 min)| 0.106±0.003                             | +42      | 0.32                          |
| 80 mM K⁺+glucose removal (20 min) | 0.191±0.009                              | +151     | 0.81                          |
| 80 mM K⁺+glucose removal (120 min) | 0.121±0.008                              | +57      | 0.78                          |

All the values were obtained after the incubation period indicated in the parenthesis. N: number of experiments for the oxygen consumption. Muscle tension is the mean value of at least 6 muscle strips and the S.E. value (less than 9% of the respective mean value) is not shown in the table. All the test values are significantly (P<0.01) higher than the control value.
Table 3. Changes in ATP content in rabbit aorta

| Condition                        | ATP content | N  | % change |
|----------------------------------|-------------|----|----------|
| Control                          | 0.70±0.04   | 15 | 0        |
| 80 mM K⁺                         | 0.65±0.03   | 6  | N.S.     |
| 154.2 mM K⁺                      | 0.51±0.05   | 6  | -27      |
| 154.2 mM K⁺+100 mM sucrose       | 0.51±0.04   | 6  | -27      |
| Glucose removal                  | 0.66±0.05   | 9  | N.S.     |
| Glucose removal+80 mM K⁺          | 0.47±0.02   | 7  | -33      |

Each value was obtained 120 min after the beginning of each incubation. N: number of experiments. N.S.: not significantly different (P>0.05) from the control value.

DISCUSSION

The basal rate of oxygen consumption in the taenia coli obtained in the present experiment (0.6 µmol/g/min) is similar to those reported earlier (14–16) and is higher than that in vascular smooth muscle (0.07–0.08 µmol/g/min; from ref. 17, and the present results). ATP contents of the resting taenia coli and aorta were also similar to those in the previous reports (for a review, see 18). A high concentration of K⁺ is known to increase the rate of oxygen consumption in various types of smooth muscle (for a review, see 19). During the maximum contraction elicited by 45.4 mM K⁺, the rate of oxygen consumption was approximately twice the rate measured in the resting muscle, supporting the previous findings by Saito et al. (14). Furthermore, a close correlation was found between muscle tension and O₂ consumption. The rate of O₂ consumption during tension development, 0.33 µmol/g tissue/min/Kg force/cm², in taenia coli is higher than that in vascular smooth muscle (0.093 µmol/g tissue/min/Kg force/cm²; from ref. 17). On the other hand, ATP content only slightly decreased during the K⁺-induced sustained contraction. Since muscle tension directly correlates with the oxygen consumption (9, 20, and the present result), the energy utilized during the sustained contraction may be mostly compensated by the increase in the rate of oxidative metabolism. K⁺-induced contraction in the taenia coli was almost completely inhibited when the ATP content decreased from the control level of 2 µmol/g to 1.6 µmol/g in the high K⁺, Na⁺-deficient solution. However, the maximum sustained contraction was maintained when the ATP content decreased down to 1.7 µmol/g in 45.4 mM K⁺ solution (Fig. 1). On the other hand, oxygen consumption was low in the high K⁺, Na⁺-deficient solution, and high in the 45.4 mM K⁺ solution. These data also support the above conclusion that only a part of the ATP stored in the tissue is utilized for muscle contraction, while the muscle cells mainly consume the ATP synthesized simultaneously by an oxidative pathway.

In the taenia coli, substituted 154.2 mM K⁺ also increased the rate of oxygen consumption, although it gradually decreased and returned to the control level within 60 min. The 154.2 mM K⁺-induced muscle tension showed a similar change. ATP content...
constantly decreased in the presence of 154.2 mM K+. Addition of pyruvate or NaCl recovered the sustained contraction and increased both the rate of oxygen consumption and ATP content. These results strongly support our previous conclusion (5) that glucose utilization is inhibited in the 154.2 mM K+, Na+-deficient solution. It has been known that glucose utilized by the taenia coli is largely derived from extracellular sources (21, 22); and in the absence of added glucose, application of NaCl had little effect on muscle tension and oxygen consumption.

Kroeger (23, 24) found in rat uteri that the substituted 127 mM K+-induced contraction reduced the rate of oxygen consumption. The explanation given for the phenomenon was that the Na pump in the tissue was inactivated in the 127 mM K+ solution containing only 23.8 mM Na+, resulting in a decreased net energy demand by the tissue and in turn decreased the energy production (23, 24). This explanation cannot be applied to the present results since addition of pyruvate, which could not activate the Na pump in the absence of Na+, increased the energy production; while addition of Na+ in the absence of added glucose, which could activate the Na pump (25), had no effect on it. Furthermore, an inhibitor of the Na+ pump, ouabain, did not abolish the increase in the rate of O2 consumption induced by pyruvate or NaCl.

In rabbit aorta, ATP content was slightly lower, but oxygen consumption was slightly higher than the respective resting levels at the 120th min of the application of the substituted 154.2 mM K+. Addition of 80 mM K+ to the glucose-depleted solution produced similar changes in both the ATP content and the rate of oxygen consumption as those found in the 154.2 mM K+ solution. Therefore, it is likely that glucose utilization is inhibited in 154.2 mM K+ solution in the aorta as is the case with the taenia coli. However, the 154.2 mM K+ solution induced only a transient contraction, while 80 mM K+ induced a maximum sustained contraction in the absence of glucose. Shibata and Briggs (26) also reported that the contractions in rabbit aorta were not affected in the absence of external glucose. A slight, but significant, increase in the rate of oxygen consumption induced by the 80 mM K+, glucose depleted solution also suggests that the aerobic metabolism in rabbit aorta is not fully dependent on external glucose. This tissue is able to utilize endogenous amino acids (27, 28), ketone bodies, and fatty acids (28) as oxidizable substrates. Sucrose added to the 154.2 mM K+ solution prevented the swelling of the muscle cell induced by the high concentration of KCl and increased the muscle tension (4). However, the sucrose application did not change the ATP content, suggesting that the swelling of the cell does not affect the metabolism.

From these results, it is concluded that high K+, Na+-deficient solution inhibits oxygen consumption and ATP production in the smooth muscle of the guinea pig taenia coli and rabbit aorta.

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