Eur J Appl Physiol (1986) 55:215–221

European Journal of
Applied Physiology
and Occupational Physiology

Metabolic and ventilatory responses to steady state exercise relative to lactate thresholds

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Summary. The metabolic and ventilatory responses to steady state submaximal exercise on the cycle ergometer were compared at four intensities in 8 healthy subjects. The trials were performed so that, after a 10 min adaptation period, power output was adjusted to maintain steady state $\dot{V}_{O_2}$ for 30 min at values equivalent to: (1) the aerobic threshold (AeT); (2) between the aerobic and the anaerobic threshold (AeTAnT); (3) the anaerobic threshold (AnT); and (4) between the anaerobic threshold and $\dot{V}_{O_{2max}}$ (AnTmax). Blood lactate concentration and ventilatory equivalents for O_2 and CO_2 demonstrated steady state values during the last 20 min of exercise at the AeT, AeAnT and AnT intensities, but increased progressively until fatigue in the AnTmax trial (mean time = 16 min). Serum glycerol levels were significantly higher at 40 min of exercise on the AeAnT and the AnT when compared to AeT, while the respiratory exchange ratios were not significantly different from each other. Thus, metabolic and ventilatory steady state can be maintained during prolonged exercise at intensities up to and including the AnT, and fat continues to be a major fuel source when exercise intensities are increased from the AeT to the AnT in steady state conditions. The blood lactate response to exercise suggests that, for the organism as a whole, anaerobic glycolysis plays a minor role in the energy release system at exercise intensities upt to and including the AnT during steady state conditions.

Key words: Aerobic threshold — Anaerobic threshold — Blood lactate — Serum free fatty acids — Serum glycerol

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Maximal oxygen uptake ($\dot{V}_{O_{2max}}$) has been classically used as an index of the capacity for prolonged exercise and as a reference point on which submaximal exercise intensities are based. Recently, the aerobic threshold (AeT) and the anaerobic threshold (AnT) have been recommended as better reference points to base submaximal exercise intensities and exercise prescription (Kindermann et al. 1979; Schnabel et al. 1982; Simon et al. 1983). According to the terminology proposed by Kindermann et al. (1979), in the blood lactate response to incremental exercise, the aerobic threshold (AeT) corresponds to the point beyond which blood lactate increases systematically above resting values (Ribeiro et al. 1985). The anerobic threshold can be identified as the second break point in the blood lactate response to incremental exercise (Ribeiro et al. 1985).

Little is known, however, about the metabolic and ventilatory responses to prolonged submaximal exercise intensities relative to the AeT and the AnT. In most studies where the responses to prolonged exercise were evaluated, the intensities were based on a certain percentage of $\dot{V}_{O_{2max}}$ (Jones et al. 1980; Scheen et al. 1981), only one intensity was studied (Kindermann et al. 1979; Schnabel et al. 1982; Stegmann and Kindermann 1982), or only one threshold was used as reference (Wasserman et al. 1967). The present study was conducted to evaluate whether steady state metabolic and ventilatory responses occur during prolonged exercise at intensities relative to the AeT and the AnT when $\dot{V}_{O_2}$ is kept constant. The metabolic and ventilatory response of 4 intensities relative to the AeT and the AnT were compared while $\dot{V}_{O_2}$ was maintained constant by adjustments in power output, to identify the level above which steady state conditions cannot be maintained.

Material and methods

Subjects. Eight healthy, physically active male subjects participated in the study. Their mean (±SD) age, height and weight were 24±3 years, 177±3 cm and 75±5 kg respectively. All subjects were informed about the possible risks and discomforts involved with the participation in the study and signed an informed consent statement. The protocol was approved by the Human Research Review Committee.

Protocol. Each of the subjects performed 6 exercise tests on an electrically braked cycle ergometer (Collins), maintaining a pedalling rate of 70 rev · min^{-1}. All tests were performed at the same time of day, after a period of at least 8 h fasting. The tests were separated by an interval of 3 to 7 days, while training programs were maintained constant, and subjects abstained from high intensity exercise for at least 12 h before the tests.

In the first exercise test a progressive incremental protocol was used for the determination of the individuals' $\dot{V}_{O_{2max}}$, AeT and AnT. In the second test, the power output corresponding to steady state $\dot{V}_{O_2}$ at the following conditions was identified: 1) the AeT; 2) the AnT; 3) the average of $\dot{V}_{O_2}$ at AeT and AnT (referred as AeTAnT); 4) the average of $\dot{V}_{O_2}$ at AnT and $\dot{V}_{O_{2max}}$ (referred as AnTmax). The other 4 exercise tests were performed in random order and were designed so that, after a 10 min adaptation period, a steady state $\dot{V}_{O_2}$ corresponding to that at AeT, AeAnT, AnT and AnTmax was maintained.

Prior to the tests an indwelling catheter was inserted in a forearm vein and was kept patent by a slow infusion of isotonic saline. Subjects breathed through a Daniels valve which directed the expired air to a mixing chamber. Inspired volume was measured by a dry gas meter (Parkinson-Cowan) and mixed expired gas concentrations were measured by calibrated CO_2 (LB2 Beckman) and O_2 analyzers (Applied Electrochemistry S3-A). Ventilatory variables were calculated on line by a microcomputer (Rockwell AIM 65 — software supplied by Rayfield Electronics). ECG were recorded continuously for determination of heart rates.

Maximal exercise test. The subjects first worked for 4 min at 30 W, then work rate was increased by 30 W per min until they were unable to maintain their pedalling rate above 40 rev · min^{-1}. During the last 15 s of each min a blood sample was drawn for determination of blood lactate concentration (Marbach and Weil 1967). $\dot{V}_{O_{2max}}$ was defined as the highest $\dot{V}_{O_2}$ attained for a period of 30 s during the test. The blood lactate values were plotted against time and three straight lines were fitted so that 2 break points were identified (Ribeiro et al. 1985). The AeT was defined as the point immediately before blood lactate levels began to increase systematically above resting values and the AnT was defined as the second break point, immediately before the rapid rise in blood lactate (Ribeiro et al. 1985). The thresholds were expressed as the corresponding $\dot{V}_{O_2}$, which was determined from a linear regression equation relating time and $\dot{V}_{O_2}$.

Submaximal tests. The subjects exercised for 3 min at an intensity requiring approximately 33% of the $\dot{V}_{O_2}$ corresponding to the specific test. This was increased to 66 and 100% of the required $\dot{V}_{O_2}$ at 3 and 6 min respectively. Using this protocol, all subjects were able to attain steady state $\dot{V}_{O_2}$ at the required level by 10 min and, when necessary, the power output of the cycle ergometer was adjusted during the test to maintain $\dot{V}_{O_2}$ within 5% of that required. Subjects were encouraged to exercise for 40 min. Blood samples were obtained for lactate concentrations, serum glycerol (Wieland 1979) and free fatty acids (Noma 1973). Heart rates were expressed as the percentage of peak heart rate attained in the maximal exercise test.

Statistical analysis. Descriptive data are presented as mean ±standard deviation (±SD). Analysis of variance for repeated measures was used to evaluate differences within and among submaximal tests. Where appropriate, the Newman Keuls method was used to perform multiple comparisons. Differences were considered significant at the probability level of 0.05.

Results

Performance

Maximal oxygen uptake of the subjects averaged 54±8 ml · kg^{-1} · min^{-1}, ranging from 45.7 to 70.5 ml · kg^{-1} · min^{-1}. Figure 1 shows that steady state $\dot{V}_{O_2}$ was maintained after 10 min of exercise in the submaximal tests at the target levels as determined in the maximal tests (dashed lines), with progressive reduction of power output. The $\dot{V}_{O_2}$ and power outputs were significantly different among the trials. All subjects were able to complete 40 min of exercise at the AeT and the AeAnT intensities. Only one subject was not able to complete 40 min of exercise at the AnT trial. Although this subject had a steady state heart rate (87% of maximal) and blood lactate levels (4.7

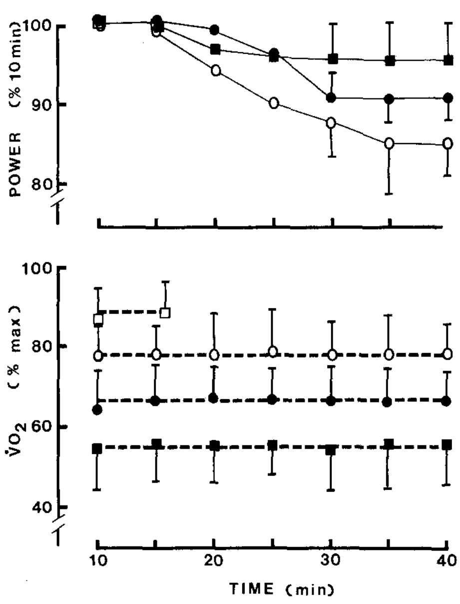

Fig. 1. Power output expressed as a percentage of the power output at 10 min of exercise (mean ±SD) at 4 intensities (top). Oxygen uptake as a percentage of $\dot{V}_{O_{2max}}$ after 10 min of exercise at 4 intensities (bottom). The dashed lines represent the $\dot{V}_{O_2}$ determined for each of the trials on the maximal exercise test. ■—■ AeT; ●—● AeAnT; ○—○ AnT; ■—□ AnTmax

mmol $\cdot l^{-1}$), he stopped at 32 min of exercise complaining of fatigue. None of the subjects was able to complete the 40 min of exercise at the AnTmax intensity. They stopped because of fatigue after 12 to 22 min of total exercise time (mean time = 16.3 ± 3.1 min).

Metabolic responses

Figure 2 presents the blood lactate responses at each of the submaximal tests. For the AeT, AeAnT and the AnT blood lactate concentration increased significantly from resting values up to 20 min of exercise, reaching a plateau thereafter. During steady state conditions the blood lactate concentration at the AnT was significantly higher than the AeT and the AeAnT. For the AnT intensity all subjects were able to maintain steady state levels during the last 20 min of exercise. For the AnTmax trial blood lactate concentration increased progressively until exhaustion.

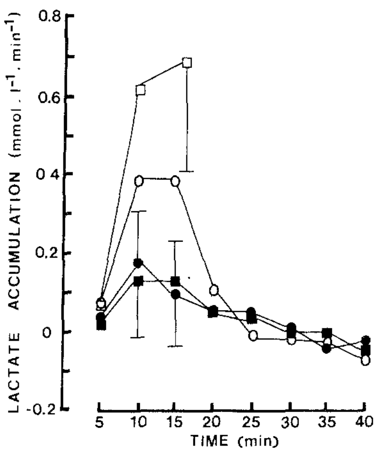

Fig. 3. Mean (±SD) blood lactate accumulation at 4 exercise intensities. Symbols as in Figure 1

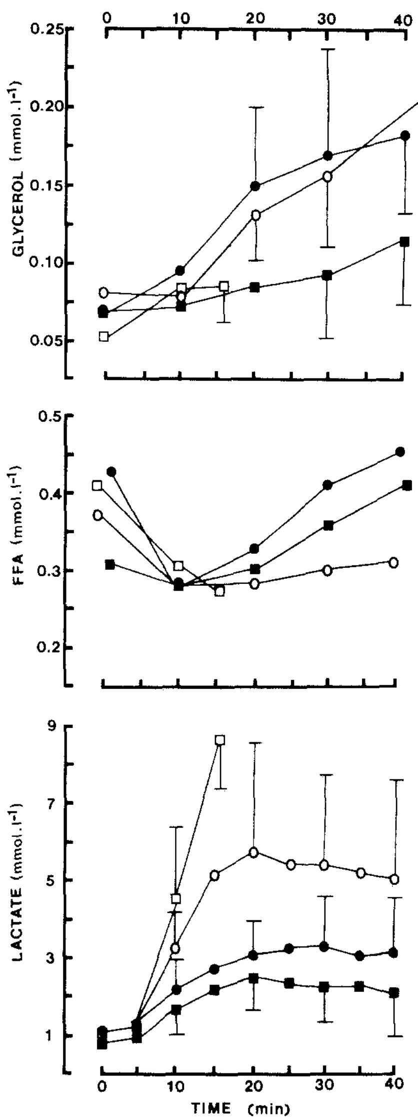

Fig. 2. Blood lactate, serum free fatty acids (FFA) and serum glycerol levels (mean ± SD) during prolonged exercise at 4 intensities. Symbols as in Figure 1

Figure 3 presents the rate of lactate accumulation in the 4 submaximal tests, calculated as the concentration at the end of the interval minus the concentration at the beginning of the interval, divided by the time period in min. It is of note that blood lactate accumulation occurred only during the initial 20 min of exercise and, even though blood lactate concentrations were higher at the AnT intensity after 20 min, accumulation was not significantly different when compared to the AeT and the AnT intensities.

Serum free fatty acid levels tended to increase after 20 min of exercise in the AeT and the AeAnT tests, showed no change at the AnT intensity, and decreased significantly from resting values during the AnTmax test (Fig. 2). However, no significant differences in serum free fatty acid levels were found between trials at different time periods. At 40 min of exercise on the AeT, AeAnT and AnT intensities, no significant correlation was found between serum free fatty acid levels and blood lactate concentrations. Serum glycerol levels increased progressively as exercise continued for all intensities. At 30 and 40 min during the tests serum glycerol levels were higher for the AeAnT and AnT when compared to the AeT.

Ventilatory responses and heart rate

The ventilatory equivalent for oxygen ($\dot{V}_E/\dot{V}_{O_2}$) reached steady state values by 10 min of exercise for the AeT, AeAnT and the AnT intensities (Fig. 4). The values during steady state were significantly higher for the AnT when compared to the AeT. During the AnTmax trial $\dot{V}_E/\dot{V}_{O_2}$ values increased progressively until fatigue. The ventilatory equivalent for carbon dioxide ($\dot{V}_E/\dot{V}_{CO_2}$) showed a response similar to the $\dot{V}_E/\dot{V}_{O_2}$, but steady state levels were reached only after 20 min of exercise.

The respiratory exchange ratio (R) increased significantly from 5 to 10 min of exercise for all intensities (Fig. 4). As exercise continued for the AeT, AeAnT and AnT, R values tended to decrease. At 10 min of exercise the AnT and the AnTmax intensities showed significantly higher R values when compared to the AeT and the AeAnT tests. Between 20 and 40 min of exercise R values were not significantly different for the AeT, AeAnT and AnT tests. For the AnTmax intensity R was similar at 10 min and at the end of the exercise.

Heart rate (HR) increased and reached steady state levels at 20 min of exercise for the AeT, AeAnT and AnT tests (Fig. 4). For the AnTmax intensity HR also increased progressively until exhaustion. During steady state exercise HR were significantly higher at the AeAnT and AnT intensities when compared to the AeT.

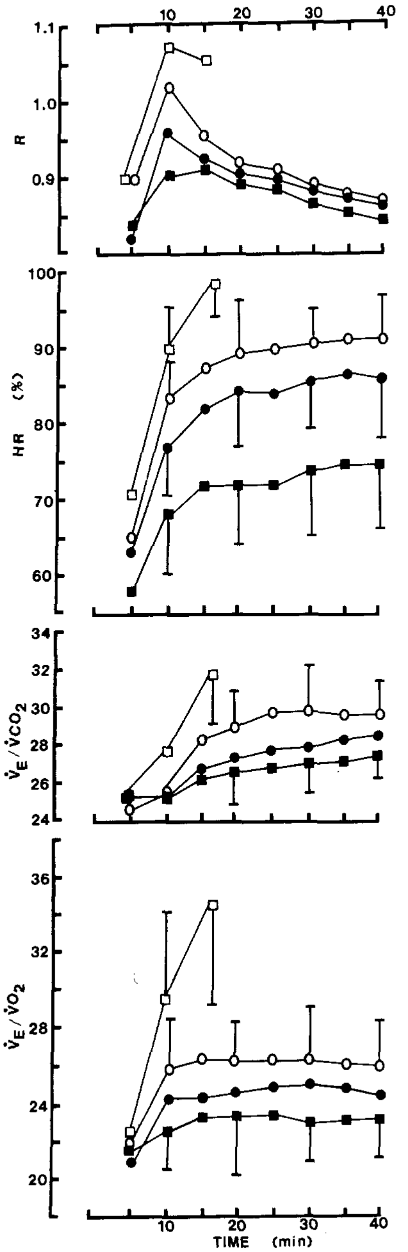

Fig. 4. Mean (±SD) values for ventilatory equivalent for oxygen ($\dot{V}_E/\dot{V}_{O_2}$), ventilatory equivalent for carbon dioxide ($\dot{V}_E/\dot{V}_{CO_2}$), heart rate as a percentage of maximal (HR), and respiratory exchange ratio (R) at 4 exercise intensities. Symbols as in Figure 1

Discussion

Protocol

The design of the present study differed from those previously reported in two ways: 1) the AeT and the AnT were identified as the $\dot{V}_{O_2}$ in the incremental exercise test corresponding to lactate break points, as opposed to the corresponding power output, since the thresholds have been shown to occur at the same metabolic rate regardless of the protocol used, but they can occur at different power outputs depending on the protocol (Ribeiro et al. 1986); 2) during steady state exercise $\dot{V}_{O_2}$ was kept constant by reducing power output when necessary (Fig. 1), as opposed to the constant power output used by other authors. Thus, our protocol, designed to evaluate a metabolic steady state, cannot be compared to others from the literature (Reybrouck et al. 1983; Scheen et al. 1981; Schnabel et al. 1982; Simon et al. 1983; Stegmann and Kindermann 1982; Wasserman et al. 1967) because of possible differences in muscle fiber recruitment patterns.

Blood lactate

If an individual exercises for long periods of time at increasing exercise intensities, a point will be reached at which blood lactate accumulation and early fatigue will occur (Bang 1936). Mader et al. (1976) proposed the use of a fixed blood lactate concentration of 4 mmol $\cdot$ l^{-1} as the level above which blood lactate accumulation should occur during continuous exercise. During the AnT submaximal test we found steady state blood lactate concentrations ranging from 2.3 to 9 mmol $\cdot$ l^{-1}, a finding which is consistent with the observations of others (Stegmann and Kindermann 1982). This indicates that steady state blood lactate levels can be maintained for long periods of time when concentrations are much higher than the level proposed by Mader et al. (1976). Moreover, if the findings of our study can be generalized for a population of normal individuals, the results of an incremental exercise test may be used to identify the metabolic rate above which lactate accumulation occurs during prolonged exercise.

If we consider the "whole body" approach proposed by Di Prampero (1981), the steady state conditions of our experiments may allow us to estimate the contribution of anerobic glycolysis for the energy release system by observing the changes in blood lactate levels (Di Prampero 1981; Seeherman et al. 1981; Wasserman et al. 1967). Accordingly, when blood lactate levels are constant, one can assume that the rate of lactate appearance equals its removal. Lactate removal by oxidation and through gluconeogenesis can be included in the aerobic fraction of the whole body energy metabolism. Thus, the net energy release from anaerobic glycolysis for the whole organism can be considered insignificant when steady state blood lactate concentrations are obtained. This was the case for the exercise intensities up to and including the AnT after 20 min of exercise (Fig. 3). Above the AnT, however, a progressive accumulation of lactate occurred, indicating that the rate of lactate appearance was higher than the rate of removal, and that the contribution of anaerobic glycolysis was appreciable. These results are consistent with the findings of Brooks et al. (1984) who, using radiotracer trechniques in rats exercising at 70% of their $\dot{V}_{O_{2\,max}}$, demonstrated that, even though blood lactate levels and lactate turnover rates were elevated, the anaerobic energy production contributed insignificantly to the total energy transduction. Margaria et al. (1964) and Seeherman et al. (1981) suggest that anaerobic glycolysis contributes significantly to the energy release system only at exercise intensities above $\dot{V}_{O_{2\,max}}$. Our data, however, suggest that the contribution of anaerobic glycolysis is appreciable at levels below $\dot{V}_{O_{2\,max}}$ and above the AnT.

A continued controversy exists on the physiological and methodological factors related to the AeT and the AnT (Brooks 1985; Davis 1985). One area of controversy is nomenclature and we now have as many terms for the thresholds as there are laboratories which study them (Jacobs 1981; Mader et al. 1976; Stegmann and Kindermann 1982; Wasserman et al. 1967). Some groups have argued that a true metabolic threshold does not exist (Brooks 1985), since lactate turnover rate has been shown to be linearly related to metabolic rate in exercising rats (Donovan and Brooks 1983). However, in the study of Donovan and Brooks (1983), the higher exercise intensity employed was lower than the AnT (as evidenced by steady state blood lactate levels). Thus, the linear relationship between lactate turnover and metabolic rate cannot be extrapolated to intensities above the AnT. Some investigators have also criticized the term "anaerobic threshold" because its literal interpretation infers a condition where oxygen is unavailable to the muscles, and evidence indicates that hypoxia is not present at submaximal exercise intensities (Brooks 1985). Our data support the contention that there is an intensity above which there is blood lactate accumulation and significant contribution of anaerobic glycolysis to the energy release system. Thus, this intensity may be appropriately named the "anaerobic threshold".

Lipid metabolism

The small increase in exercise intensity from the AeT to the AeAnT resulted in a significant increase in serum glycerol levels (Fig. 2). This increase in serum glycerol without changes in serum free fatty acid concentration may reflect stimulation of muscle lipolysis and utilization of endogenous triglycerides as fuel, since hepatic uptake of glycerol is increased at higher exercise intensities, despite reduction in heptatic blood flow (Jones et al. 1980; Wahren et al. 1971). This hypothesis is supported by the finding of similar respiratory exchange ratios (R) for the AeT, AeAnT and AnT intensities. Since during steady state conditions R is thought to reflect the respiratory quotient, this indicates that fat oxidation continued to contribute significantly as a fuel when the exercise intensity was increased from the AeT to the AnT.

Elevated blood lactate levels may inhibit free fatty acid turnover (Issekutz et al. 1975). Since the increase in uptake and oxidation of free fatty acids by skeletal muscle is due to a mass action effect (Armstrong et al. 1961), one would expect fat oxidation to decrease at exercise intensities above the AeT, when blood lactate concentration increased. This was not the case in the present experiments and we found no correlation between blood lactate concentration and free fatty acid levels. Elevated plasma catecholamines are a potent stimulus for lypolysis (Havel et al. 1964), and Schnabel et al. (1982) have shown evidence for a continuous increase in plasma norepinephrine during steady state conditions at the AnT. Thus, sympathetic stimulation of lypolysis could have overdriven the inhibitory effects of elevated blood lactate levels.

Ventilatory responses

In an incremental exercise test, the hyperventilation that occurs above the AeT is thought to be dependent (among other factors) on the excess $\dot{V}_{CO_2}$ derived from the buffering of lactic acid by the bicarbonate system (Davis 1985). Considering the AnT intensity of our experiments, during the first 10 min of exercise $\dot{V}_E/\dot{V}_{O_2}$ increased significantly, while $\dot{V}_E/\dot{V}_{CO_2}$ did not change, since the increase in ventilation was proportional to the increase in $\dot{V}_{CO_2}$. This is in agreement with the response predicted for incremental exercise tests between the AeT and the AnT (Davis 1985). During the steady state part of the trial $\dot{V}_E/\dot{V}_{O_2}$ remained constant, while $\dot{V}_E/\dot{V}_{CO_2}$ increased between 10 to 20 min of exercise and remained constant thereafter. This increase in $\dot{V}_E/\dot{V}_{CO_2}$ occurred because of a decrease in $\dot{V}_{CO_2}$ (as indicated by a reduction in R), with constant levels of $\dot{V}_E$. This elevated steady state $\dot{V}_E$ at the time when $\dot{V}_{CO_2}$ was decreasing has to be explained by the interaction of other factors, including acidosis (Reybrouk et al. 1983), increase in body temperature (Martin et al. 1979) and elevated plasma catecholamines (Schnabel et al. 1982).

Conclusions

The present study demonstrated that steady state blood lactate levels as well as ventilatory responses may occur at exercise intensities up to an including the AnT during prolonged exercise at constant metabolic rate. At intensities above the AnT, lactate accumulation and ventilation progressively increase with early onset of fatigue. A similar respiratory exchange ratio together with higher serum glycerol levels that occur when exercise intensities are increased from the AeT to the AnT indicate that fat continued to be a major source of fuel. The lack of blood lactate accumulation between 20 and 40 min of steady state exercise at intensities up to and including the AnT suggests that anaerobic glycolysis plays a minor role in the release of energy for the whole organism.

Acknowledgements. Dr. Ribeiro was supported by fellowship number 3660/80-3 from CAPES and by the Federal University of Rio Grande do Sul (Brazil). The authors are grateful to Dr. Richard P. Adams and Dr. John Young for the review of the manuscript.

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Accepted January 16, 1985