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COMPOSITION OF THE SECRETION FROM THE ECCRINE SWEAT GLANDS OF THE CAT'S FOOT PAD

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SUMMARY

1. The sweat composition from the cat's foot pad was examined at various rates of secretion. Sodium pentobarbitone or chloralose anaesthesia were used.

2. Cat's pad sweat contains lactate, glucose is almost absent, and the sodium and chloride concentrations increased with increasing sweat rate. In these respects the secretion resembles human eccrine sweat.

3. The sodium, chloride, and potassium concentrations are much higher than in human sweat; also the potassium level decreased with increasing rate. Consequently, whereas human sweat is hypotonic with respect to the plasma, cat's pad sweat is slightly hypertonic with respect to the plasma even at low rates of secretion. In contrast to human sweat glands, which produce a slightly acidic secretion containing ammonia, cat's pad sweat glands produce an alkaline secretion containing bicarbonate. Also in contrast to human sweat, lactate levels decreased with increasing sweat rate.

INTRODUCTION

All investigations carried out so far on the chemistry of eccrine sweat secretion have been on man (for reviews see Rothman, 1954; Robinson & Robinson, 1954). Despite the large mass of information on the composition of human sweat and factors affecting it (Rothman, 1954; Robinson & Robinson, 1954; Weiner & Hellman, 1960), our understanding of the detailed mechanism of sweat formation remains rudimentary (for discussion see Schwartz, 1960). Investigation of these questions in man is greatly limited by the extent to which the glands can be subjected to experimental interference. Some of these limitations would not apply to a suitable animal preparation, and for this reason it was decided to use the eccrine glands of the hairless pad of the cat's foot for further investigations of the processes

of sweat formation. As an essential preliminary the composition of cat's pad sweat at various rates of secretion has been studied and is reported in this paper.

METHODS

Sweat secretion was elicited by stimulation of the lateral branch of the internal plantar nerve in the hind leg using a 10 V stimulus and pulse duration of 0·3 msec. The sudomotor fibres in this nerve innervate the central pad (Wang & Lu, 1930; Collins, 1960) and from this area sweat was collected. An intact circulation was maintained.

In one series of experiments the cats were anaesthetized with sodium pentobarbitone, whilst in another series chloralose was used.

A small oval-shaped capsule fitted with inlet and outlet tubes was stuck on to the central portion of the central pad. (Capsules of similar design, but of different areas, were constructed, the area of the capsule used depending on the size of the pad; the areas of the capsules varied from approximately 0·2 cm^2 to approximately 0·5 cm^2.) To make the capsule secure a metal ring was fixed around the whole pad. The small capsule was then clamped into position by means of four screws in the metal ring (Fig. 1).

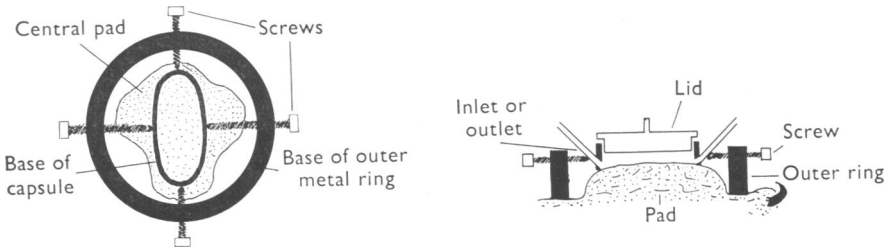

Fig. 1. Sectional diagrams of capsule together with outer metal ring.

Dry nitrogen was passed through the capsule so that there was immediate evaporation of any sweat present. The nitrogen (with any evaporated sweat) was then passed through an infra-red analyser and finally a flowmeter. The response of the analyser is proportional to the amount of water vapour in the nitrogen passing through it. The analyser was calibrated by introducing known volumes of water into the circuit. The volumes of sweat secreted were determined by reference to the calibration graph for the corresponding rates of gas flow. At the higher rates of secretion a gas flow of 1 l./min was used; 0·5 and 0·3 l./min were used at lower rates.

A reading was obtained just by passing the nitrogen through the conducting system. Since dry nitrogen was being passed over the skin (Buettner, 1953) there would also be an appreciable diffusion of water vapour through the skin. At room temperature the reading due to insensible perspiration was similar in magnitude to that due to just passing the gas through the conducting system, and, of course, superimposed upon it. A steady base line was, therefore, always obtained before the start of a collection, and at the cessation of stimulation the recording was always allowed to return to the original base line.

With this method a continuous monitor could be kept of the amount of sweat produced throughout secretion. As the sweat evaporates immediately it is formed the re-absorption of water at the skin surface (Buettner, 1953) is reduced to a minimum.

By removing the detachable lid of the capsule, solutes could be washed off the skin with distilled water. Account was taken of any small blank readings obtained from merely washing the pad, and frequent blank washings were made.

Owing to the small area of the capsule a relatively long stimulation period was necessary in order to obtain enough sweat for reliable analysis. The glands were, therefore, stimulated

for 30 min from the start of secretion, and then rested for about 1 hr, during which period the pad was washed and a blank washing usually taken for analysis. The order of th stimulation frequencies was varied from cat to cat.

The washings were analysed for sodium and potassium by flame photometry, chloride by potentiometric titration, lactate by the method of Barker & Summerson (1941), ammonia by the method of Russell (1944) for earlier samples and the Fawcett & Scott (1960) method for later samples. These substances are quantitatively the most important ions in human sweat (Foster, 1961).

The washings were also analysed for bicarbonate for two reasons: (*a*) summation of the above mentioned ions left a large anionic deficit to be accounted for, and (*b*) the sweating skin surface was found to be extremely alkaline (of the order of pH 9, measured by placing an indicator paper on the skin surface). Warburg manometers with micro flasks were used to determine the bicarbonate in the samples obtained from most of the cats anaesthetized with pentobarbitone. The more sensitive and reliable van Slyke micro-manometric method (van Slyke & Plazin, 1961) was used on the samples from the chloralose-treated cats.

Glucose was also determined in the pad sweat from both a chloralose- and pentobarbitone-anaesthetized cat by the method of Horvath & Knehr (1941).

In some cases blood was taken at the end of the experiment by cannulating the carotid artery. In some cats samples were also taken after each collection. The samples were heparinized and immediately centrifuged, and the plasma was removed. The sweat samples and the plasma were stored in plastic containers at −4° C. For bicarbonate analyses the blood was collected under oil.

Osmotic pressure measurements were made using a Fiske thermistor osmometer.

RESULTS

Secretion of fluid

The latency of response, as shown by the infra-red analyser, was very variable, ranging from less than $\frac{1}{2}$ min to over 2 min. An analysis of variance of the latencies obtained from ten cats showed that the latency increased with decreased frequency [$F(1, 47) = 26{\cdot}0$, $P < 0{\cdot}001$]. Although there was some variation in the initial form of the response, the rate of secretion in the majority of instances rose sharply at first and then gradually levelled off to a plateau (Fig. 2). This was usually reached 4–6 min after the start of secretion and was maintained for as long as the nerve was stimulated, although a gradual decline in rate sometimes occurred. On cessation of stimulation the response fell off steeply at first and then gradually tailed away.

The latency probably mostly represents the time needed for filling the sweat ducts. The response time of the recorder to the presence of water in the capsule at a gas flow of 1 l./min was only 2–3 sec. The initial shape of the curve could be due to: (1) the variation in the activity of the secretory cells in different glands resulting in variable filling times of the ducts (Lloyd, 1962), (2) the gradual, if slight, wetting of the skin surface; (3) the equilibration of the conducting system.

The shape of the decline in the recording after the cessation of stimulation could be due to: (1) the removal of transmitter substance remaining

at the end of stimulation; (2) the drying out of the conducting system and skin surface; (3) the expulsion and evaporation of water remaining in the ducts at the end of stimulation.

The relation between sweat rate and frequency of stimulation is shown in Fig. 3 for five different cats. It can be seen that the sweat rate was linearly related to frequency at the lower stimulation rates. The increase

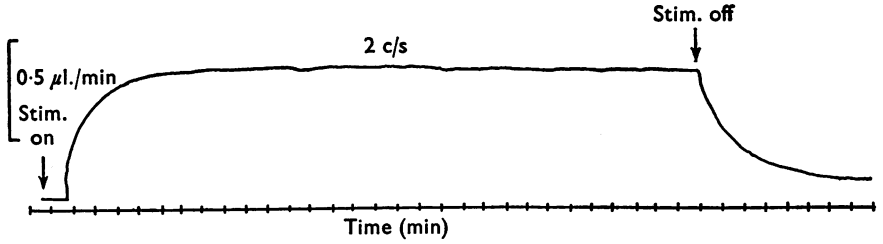

Fig. 2. Response of cat's foot pad sweat glands to plantar nerve stimulation. Response measured by passing evaporated sweat from central pad of hind foot through an infra-red analyser.

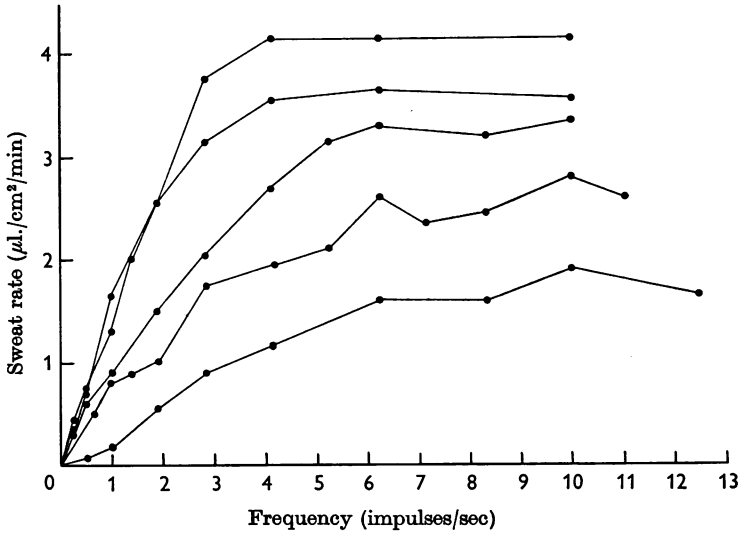

Fig. 3. Relation between rate of secretion from foot pad sweat glands and frequency of stimulation of plantar nerve for five different cats.

in the sweat rate then gradually fell off as the maximum secretory rates were reached at frequencies which varied from 4–6 c/s up to 10 c/s. The maximum secretory rate varied considerably from cat to cat. Glands of very young cats usually responded well. Glands of mature cats, on the other hand, frequently either failed to respond at all or could only be made to secrete at relatively low rates.

Composition of secretion

Variations in the concentrations of the constituents in relation to sweat rate for cats under pentobarbitone are shown in Fig. 4. Sodium analyses were from fifteen cats, potassium analyses from fourteen cats, chloride and bicarbonate analyses from seven cats, and lactate analyses from six cats. Six samples were nearly always obtained from each cat.

Samples from another four cats anaesthetized with chloralose were

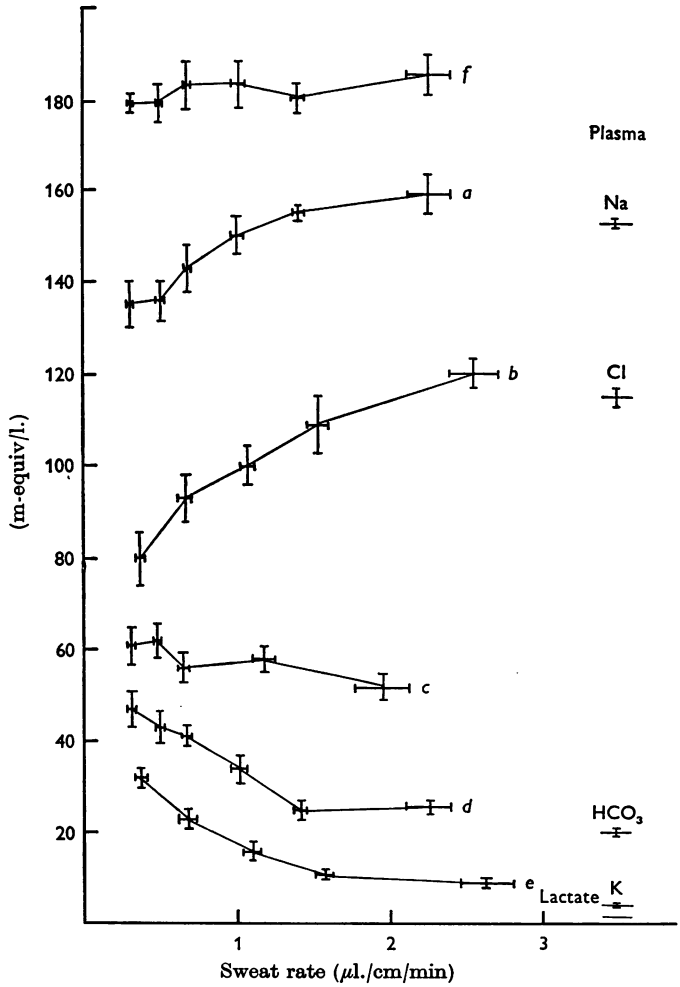

Fig. 4. Variations in the concentrations of *a* sodium, *b* chloride, *c* bicarbonate, *d* potassium and *e* lactate in cat's pad sweat with rate of secretion. Mean values (± S.E.) of rates, concentrations, and plasma levels are shown. The sum of the potassium and sodium concentration *f* is also given.

analysed for sodium, potassium, chloride, bicarbonate and lactate, six samples being collected from each cat.

High sodium concentrations were obtained compared to those found in human sweat. The concentration in most cats decreased with decreasing sweat rate from about plasma level at the highest rates to well below plasma level at the lowest rates measured. The potassium concentration usually increased with decreasing sweat rate, varying from about 3 to 8 times plasma level at the highest rates to as much as 20 times plasma level at the lowest rates. The chloride concentration, like sodium, was usually approximately that of the plasma at the highest sweat rates, decreasing with decreasing rate to well below plasma level at the lowest rates of collection. Lactate levels always increased with decreasing rate, the lowest concentrations at maximum rates, as with potassium, always being well above that of the plasma. Bicarbonate was present in concentrations between two and four times that of the plasma (mean plasma value = 20/m-equiv/l). In contrast to human sweat, ammonia could not be detected in the sweat of the cat's pad.

Whilst the majority of the results conformed to the pattern outlined above, there were a number of differences in some cats. In one pentobarbitone- and two chloralose-treated cats the sodium and chloride concentrations rose above plasma level at the highest rates; and the sodium and chloride concentrations from these two chloralose cats also increased again at the lowest rates so that the concentration did not fall appreciably below plasma level. In two cats under pentobarbitone the sodium concentration did not vary appreciably from plasma level, whilst the sodium levels in another such cat which showed no variation with rate tended to be above plasma level. No variation in potassium concentration with rate occurred in two similarly anaesthetized cats.

Taking all the results, the regression of the concentration of each constituent on sweat rate was determined by analysis of variance. Highly significant trends were obtained for sodium [$F(1, 104) = 29{\cdot}7$, $P < 0{\cdot}001$], potassium [$F(1, 97) = 31{\cdot}1$, $P < 0{\cdot}001$], chloride [$F(1,58) = 27{\cdot}8$, $P < 0{\cdot}001$], as well as lactate [$F(1, 57) = 56{\cdot}5$, $P < 0{\cdot}001$]. None of these trends showed any significant departure from linearity. Hence, despite the deviations that occurred in some cats, a tendency for the sodium and chloride concentrations to decrease with decreased rate, and the potassium and lactate concentrations to increase with decreased rate, was still evident. There may have been some tendency for the bicarbonate concentration to increase with decreased rate, the linear trend between concentration and rate being significant [$F(1, 64) = 5{\cdot}1$, $P < 0{\cdot}05$].

Correlations were obtained between the sodium and potassium concentrations for both the chloralose and pentobarbitone results. At the level

$P < 0{\cdot}05$ there was no difference between the pentobarbitone and the chloralose results for the slopes of the regressions of sodium on potassium. The highly significant linear relation [$F(1, 97) = 97{\cdot}0$, $P < 0{\cdot}001$] for all the results is shown in Fig. 5. This relation showed no departure from linearity and the slope of the regression did not differ from -1 at the level $P < 0{\cdot}05$. Because of this inverse relation between sodium and potassium the total measured cation concentration showed no significant variation with rate, the mean value ($\pm$ S.E. of mean) of the measured cation concentration for all the results being $181 \pm 1{\cdot}3$ m-equiv/l. The value of this mean indicated that the secretion was slightly hypertonic with respect to the plasma.

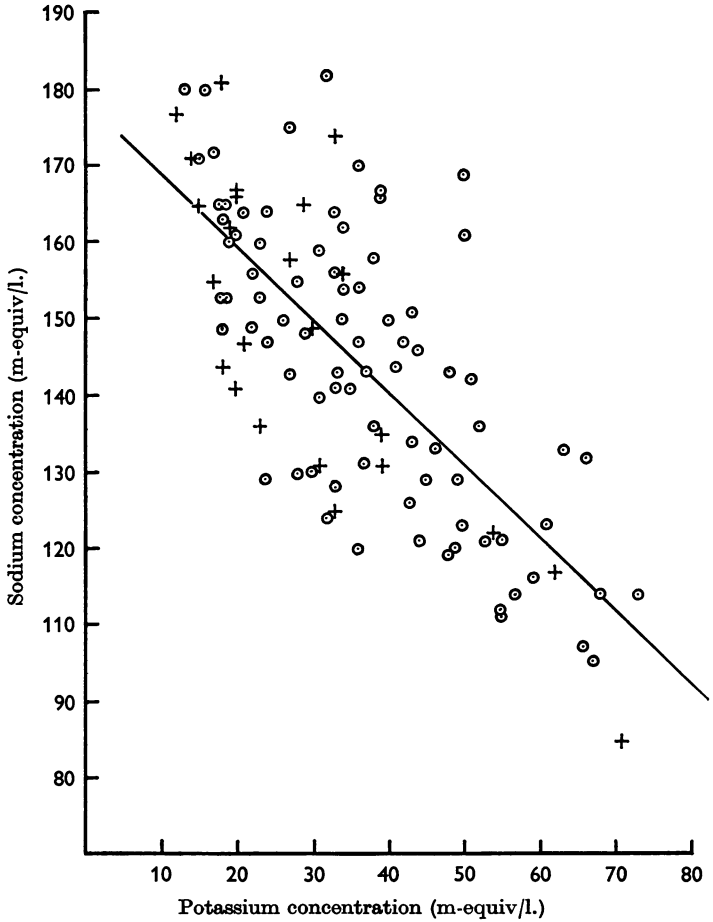

Fig. 5. Relation between sodium and potassium concentrations. $Y = -0{\cdot}9645X + 179{\cdot}3$. The 95% confidence limits of the slope of this regression are $\pm$ 0·1734. (⊙pentobarbitone results; + chloralose results).

In order to determine the osmotic pressure of the secretion six samples of the order of 50–100 μl. were collected. The osmolalities of the washings (approximately 400 μl. for each sample) and the plasma were measured. The washings were also analysed for sodium and potassium. As the washings upon which the osmotic pressure measurements were made represented diluted forms of the secretion, the osmolalities were corrected to account for changes in the activities of the constituents with dilution. The mean sodium concentration ($\pm$ S.D.) was $161 \pm 4{\cdot}3$ m-equiv/l. compared with only $25 \pm 5{\cdot}4$ m-equiv/l. for potassium. The solutions were, therefore, for the purpose of making these corrections considered to be pure sodium chloride solutions. The values of the molal osmotic coefficients for sodium chloride solutions equivalent to the total measured cation concentrations of the diluted and undiluted samples were obtained from *Electrolyte Solutions*, by Robinson & Stokes (1955), and the measured osmolalities were adjusted accordingly. The mean osmolality ($\pm$ S.D.) of the samples thus determined was $347 \pm 13{\cdot}9$ m-osmoles, and the mean plasma osmolality ($\pm$ S.D.) was $308 \pm 8{\cdot}5$ m-osmoles. The difference between the sweat and plasma osmolalities was significant [$t_5 = 5{\cdot}3$, $P < 0{\cdot}01$]. Calculating the osmotic pressures of these samples by the relation $\Pi = [C] \times \phi \times 2 + N$, where Π = m-osmoles, $[C]$ = total measured cation concentration in m-equiv/l., ϕ = molal osmotic coefficient for a sodium chloride solution at concentration $[C]$, and N = m-moles/l. of urea present (assumed to be about eight from unpublished data on other samples), the mean value ($\pm$ S.D.) for all the samples was $352 \pm 12{\cdot}1$ m-osmoles.

Correlations were obtained between the sodium and chloride concentrations for both the chloralose and pentobarbitone results. At the level $P < 0{\cdot}05$ there was no difference between the chloralose and pentobarbitone results for the slopes of the regressions of sodium on chloride. The highly significant linear relation [$F(1, 58) = 78{\cdot}9$, $P < 0{\cdot}001$] for all the results is shown in Fig. 6. This relation showed no departure from linearity.

Again the linear regression of potassium concentration on lactate concentration for all the results was highly significant with no departure from linearity. However, whilst the slope of the linear regression for all the pentobarbitone cats (Fig. 7) did not differ at the level $P < 0{\cdot}05$ from the slope of the regression for one of the chloralose cats, it was significantly greater at this level than the slope of the regression for the other three chloralose cats.

After subtracting the sum of the measured anions from the sum of the measured cations there usually remained an anionic deficit. The mean value of this deficit ($\pm$ S.E. of mean) for all the results was $6{\cdot}5 \pm 1{\cdot}5$ m-equiv/l. Whilst the value of this deficit was statistically significant, it is possible

that analytical errors could account for a discrepancy of this magnitude. Samples were analysed for phosphate but none could be detected.

Glucose was not present in the sweat of either the chloralose or pentobarbitone cats in substantial quantities. The average value found was 5 mg/100 ml.

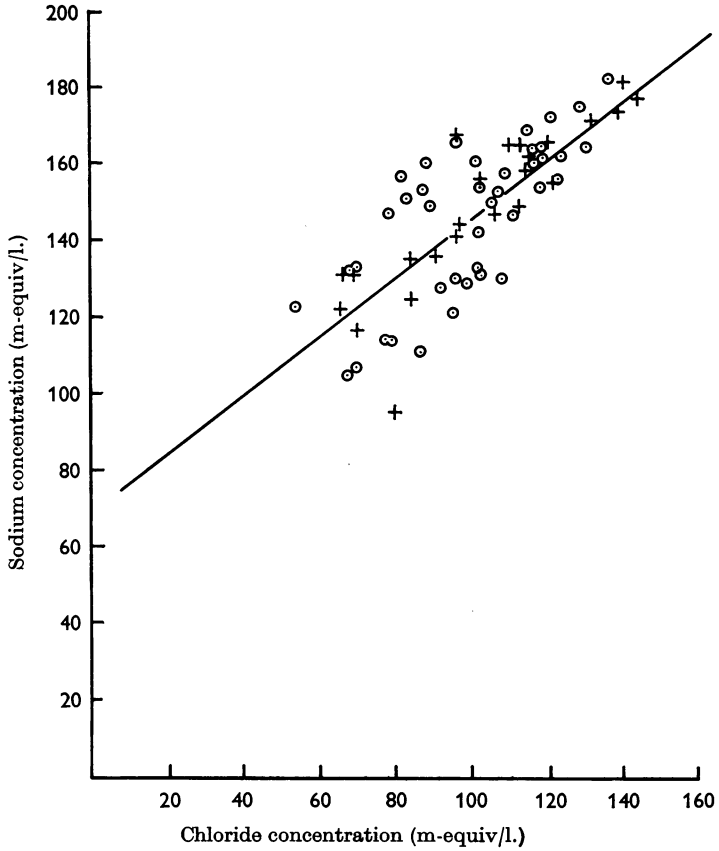

Fig. 6. Relation between sodium and chloride concentrations. $Y = 0{\cdot}7638X + 70{\cdot}0$. The 95% confidence limits of the slope of this regression are $\pm$ 0·1496. (⊙ pentobarbitone results; + chloralose results).

DISCUSSION

The usual ionic composition of the secretion was sodium and chloride concentrations approximately at plasma level, and potassium, lactate, and bicarbonate concentrations several times greater than plasma level at maximum rates. Then with decreasing sweat rate the sodium and chloride concentrations decreased, and the potassium and lactate concentrations increased. There may have been a small increase in the bicarbonate con-

centration with decreasing rate. Whilst there were deviations from this pattern of behaviour in some cats certain ionic interrelations still tended to occur. Thus, little or no variation in the sodium concentration with rate was reflected by little or no variation in the potassium concentration;

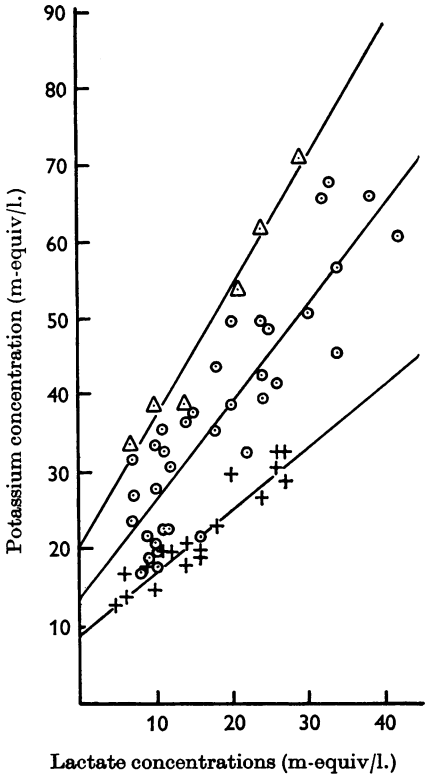

Fig. 7. Relation between potassium and lactate concentrations. Pentobarbitone results (⊙) $Y = 1{\cdot}3180X + 13{\cdot}7$. Chloralose results, one cat (△) $Y = 1{\cdot}704X + 20{\cdot}0$. Chloralose results, three cats (+) $Y = 0{\cdot}8145X + 9{\cdot}3$.

similarly, larger decreases in the sodium concentration with decreasing rate were accompanied by larger increases in the potassium concentration, so that a highly significant linear regression was obtained between these two constituents, the slope of which did not differ significantly from -1 at the level $P < 0{\cdot}05$. Also, although the chloride concentration was not measured in those cats under pentobarbitone where there was no general trend in the sodium concentration with rate, it seems likely from the linear regression obtained between the sodium and chloride concentrations that there would be little or no variation in the level of this component with rate in these cats.

If the deviation of the secretion's ionic composition from plasma composition is taken as a measure of the glands' ability to perform work, then it would seem that the more the glands conformed to the general type of behaviour outlined above (i.e. the higher the potassium and lactate concentrations at any given rate, and the lower the sodium and chloride concentrations at this rate compared to plasma level) the more actively the glands were functioning. In the case of the relation between potassium and lactate, the slope of the regression may be a measure of the 'efficient' functioning of the glands. Hence in three of the chloralose cats, when the potassium level tended to be lower than that found in the majority of the pentobarbitone cats and in the other chloralose cat (in two of these three cats the sodium and chloride levels did not fall below plasma level), the slope of this regression was significantly lower (at the level $P < 0{\cdot}05$) than the slopes of this regression for the other chloralose cat and all the pentobarbitone experiments.

Lactate was only measured in one cat under pentobarbitone with relatively low potassium and high sodium levels. A regression with a similarly reduced slope may have also been obtained for all the 'anomalous' pentobarbitone results. It is, therefore, not possible to say from these results whether chloralose specifically had a tendency to interfere with active cellular processes in the glands. The factor, or factors, responsible for the 'anomalous' results is not known. Whilst the effect of either anaesthetic cannot be ruled out, it is possible that dietary factors may be of some significance.

Comparison between human and cat's pad sweat

Although the compositions of cat's pad and human eccrine sweat are similar in some respects, there are a number of striking differences between the two secretions. The sodium and chloride levels in cat's pad sweat tend to be much higher than in human sweat, the concentrations of these two constituents in both thermogenic and palmar (Collins, 1962) sweat always being well below plasma level. Only at the lowest measured rates in cat's pad sweat did the levels of sodium and chloride approach values obtained in human sweat. The excess of sodium over chloride is much greater in cat's pad sweat than that of man (Robinson & Robinson, 1954; Collins, 1962). The potassium concentration in human sweat produced in response to thermal stimuli (Collins, 1962) is of the same order as that of the plasma; and even that produced in response to methacholine (Collins, 1962; Schwartz & Thaysen, 1956), which has a higher potassium concentration than the plasma, is much more dilute than cat's pad sweat in this constituent. Further, the potassium concentration of methacholine-stimulated sweat does not apparently vary with rate (Schwartz & Thaysen, 1956).

Thermogenic human sweat contains no bicarbonate, but may contain appreciable quantities of ammonia, and its pH is usually acidic (Robinson & Robinson, 1954). Cat's sweat is quite different in these respects, ammonia being absent and large quantities of bicarbonate being present.

In both thermogenic (Schwartz & Thaysen, 1956) and cat's pad sweat there is usually a decrease in sodium and chloride concentrations with decreased rate. The sweat glands of both man and cat possess very efficient mechanisms either for preventing glucose from entering the secretion or for reabsorbing glucose from the secretion. Lactate is present in thermogenic human sweat (Robinson & Robinson, 1954) and cat's pad sweat in similar concentrations, although the lactate concentration in human sweat does not appear to vary with rate (Weiner & van Heyningen, 1952; Åstrand, 1963). The lactate content of palmar sweat (Collins, 1962) is much higher than that found in cat's pad sweat.

The potassium/lactate ratio in thermogenic and palmar sweat (Collins 1962) is less than unity, whereas this ratio is greater than unity in the cat. The level of sodium chiefly determines the osmotic pressure of human thermogenic sweat at all rates. Thermogenic human sweat, therefore. when properly collected (van Heyningen, 1951) is always hypotonic with respect to the plasma, and the tonicity of the secretion decreases with decreasing sweat rate. Cat's pad sweat, on the other hand, because of the high sodium and potassium levels and the inverse relation between these constituents, would appear always to be hypertonic with respect to the plasma.

In periods of intense sweating in man large volumes of fluid can be lost by the sweat, and in the absence of adequate intakes of salt and water very serious disturbances to the electrolyte and water balance of the body can occur. If large quantities of bicarbonate were secreted in man, as in the cat, serious disturbances in the acid/base balance of the body could occur with prolonged periods of intense sweating. The hypotonic nature of the secretion together with the complete absence of bicarbonate help, therefore, to keep disturbances in the electrolyte balance of the body to a minimum. In the cat, however, the amount of sweat that can be produced is so insignificant compared to the total body-fluid volume that whatever its composition the changes in body-fluid composition due to sweating must be negligible.

The pH of sweat

In the alkalinity and high bicarbonate content of its sweat the cat stands in sharp contrast to man. It may be thought that the high sweat bicarbonate level recorded in the cat's pad secretion is the result of disturbance in the acid/base balance of the body fluids during the experimental period. In dog's parotid saliva the level of bicarbonate appears to depend on both the plasma bicarbonate level and on the arterial P_{CO_2} (Burgen & Emmelin

1961). When the plasma bicarbonate alone is raised the saliva bicarbonate increases but the saliva/plasma ratio of this ion does not change. When the arterial P_{CO_2} is increased the saliva bicarbonate increases, so increasing the saliva/plasma ratio. In the anaesthetized cat the plasma bicarbonate values (mean value 20 m-equiv/l.) were always low compared with normal human plasma levels and in man such values would be indicative of either a respiratory alkalosis or a metabolic acidosis. If, therefore, the cats were not in normal acid/base balance and the above relations for saliva applied equally to sweat, then the sweat bicarbonate is likely to be even higher when the cats are in normal acid/base balance.

Although no ammonia could be detected in the sweat this does not mean that it may not be present in the secretion originally. The sweat must certainly be on the alkaline side of neutrality when secreted, owing to the presence of the large quantities of bicarbonate. With evaporation, dissolved CO_2 would be lost and the pH would rise. Hence the pH value of approximately 9 obtained by placing an indicator paper on the sweating skin surface. Any ammonia originally present in the secretion would tend to be evolved at such a high pH. It seems improbable, however, that ammonia would be secreted in the presence of the large quantities of bicarbonate found.

Human sweat glands must possess an effective and very powerful mechanism either for preventing bicarbonate from entering the secretion or for reabsorbing secreted bicarbonate. Can human sweat glands be made to secrete bicarbonate? Amatruda & Welt (1952) in a somewhat inconclusive experiment studied the effect of an induced alkalosis on sweat composition. Bicarbonate was not measured, but according to the slight ionic changes that occurred it is doubtful if significant amounts could have been secreted.

It would seem, therefore, that human sweat glands are oriented towards producing a slightly acidic secretion containing ammonia, whereas cat's pad sweat glands are oriented towards producing an alkaline secretion containing bicarbonate.

Osmolality of the secretion

Although the osmolality of the secretion was not measured directly, and its determination involved making an approximation, the error involved is likely to be very small. It is highly probable, therefore, that the secretion is slightly hypertonic with respect to the plasma. Further, although osmotic pressure measurements were only made on secretions produced at maximum rates, because of the inverse relation between sodium and potassium it is again highly probable that the secretion remains hypertonic at all rates.

There was no significant difference between the osmolalities calculated from the measured cation concentrations and those obtained from measuring the osmolalities of the washings. Although these calculations also involved making approximations, the possible error involved is again not likely to be of any significance. The extreme closeness of these results indicates that virtually all the osmolality of the secretion can be accounted for in terms of the measured constituents.

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