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REGIONAL AND INDIVIDUAL VARIATIONS IN THE FUNCTION OF THE HUMAN ECCRINE SWEAT GLAND*

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ABSTRACT

Derived values for sodium concentration of the precursor fluid, free water clearance and counts of the number of active sweat glands were determined on the forehead, forearm and back of 14 subjects. Maximal sweat rate per gland and maximal free water clearance per gland were also calculated. The sodium concentration of the precursor fluid averaged 140 mEq/L. The large variations among our subjects in the maximal sweat rate (SR max) per m^2 and maximal free water clearance (FWC max) per m^2 depended mainly on differences in the functional capacity of individual sweat glands rather than in differences in population. However, regional variations in SR max per m^2 and FWC max per m^2 in each subject depended largely on differences in the population of active sweat glands. A significant correlation was found between secretory (SR max per gland) and reabsorptive capacity (FWC max per gland).

The secretory cells of the human eccrine sweat gland elaborate an isotonic precursor fluid. Ductal reabsorption of sodium in excess of water produces sweat whose sodium content is hypotonic to plasma (1–4). The interrelation between secretory and reabsorptive function is not known, although the secretory process is enhanced by sweat gland training, either thermally or pharmacologically (5), and the reabsorptive process is increased after salt depletion (6) or after the administration of mineralocorticoids (7, 8).

The capacity to sweat differs greatly from person to person as does the sodium chloride content of the sweat (6). Even within a given individual, there are regional variations in sweat rate and sodium chloride content (9, 10). However, it has not been fully established whether these variations result from regional differences in the population of sweat glands or from the function of single sweat glands within a given area or a combination of these two factors.

With these questions in mind, we have estimated the secretory and reabsorptive capacity of single sweat glands.

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MATERIALS AND METHODS

1. *Sodium reabsorption by the sweat duct.* The most practical method to determine ductal sodium reabsorption indirectly was originally proposed by Schwartz and Thaysen (11) and later modified by Cage and Dobson (4). When rates of sodium excretion (y) are plotted against sweat rates (x), an essentially linear function is obtained at higher sweat rates. An extrapolation of this straight line gives a positive intercept on the x axis and a negative intercept on the y axis. If it is presumed that all reabsorption in the duct is dependent upon active sodium reabsorption which has a transfer maximum, then the linear portion of the curve represents points which exceed this transfer maximum (11). Since no additional reabsorption is occurring above this range, then the slope of this straight line must equal the sodium concentration of the secretory fluid. The negative "y" intercept would then equal the maximum rate of water-free sodium reabsorption by the duct and the positive "x" intercept would be a measure of the maximum free water clearance. Since the maximum free water clearance (FWC max) is proportional to maximum water-free sodium reabsorption, FWC max was used as an index of sodium reabsorption by the duct in this study.

2. *Sodium concentration of the precursor fluid.* The sodium concentration of the precursor fluid was shown to be isotonic to plasma by Schulz et al (1) by means of a direct micropuncture technique and by Slegers (2), who used a cryoscopic method. However, Schwartz and Thaysen (11), with their method of analysis, found the average value in normal adults to be 56.5 mEq/L with a range of 7 to 96 in mecholyl-induced sweat. Gibson and di Sant'Agnese (12) later found an average value of 95 mEq/L in adults and 62 mEq/L in children in pilocarpine-induced sweat.

These low values for the sodium concentration of the precursor fluid are contradictory to the observations of Schulz et al (1) and Slegers (2) and almost invalidated the applicability of Schwartz and Thaysen's method for estimating sweat gland function until Cage and Dobson (4) proved the validity of this method by showing the concentration of the precursor fluid of thermally induced sweat to be 137.8 mEq/L which is distinctly in the isotonic range.

In our experience this method is satisfactory if the following conditions are fulfilled:

a. Sweat must be induced thermally since the electrolyte content of pharmacologically-induced sweat differs from thermal sweat (13).

b. The sweat rate must be sufficiently high since even a maximal sweat rate occasionally does not achieve a linear function.

c. Any leakage of sweat into the test site from the surroundings must be prevented since this tends to lower the derived values for the sodium concentration of the precursor fluid. A leakage-free sweat collection chamber we recently developed has eliminated this difficulty (14).

3. *Experimental procedures.* Seventeen male medical students, aged 22 to 25, were used as experimental subjects. Of these, three subjects failed to produce a sufficiently high sweat rate and were excluded from the study. The entire experiment was performed between late autumn of 1968 and early spring of 1969. Vigorous physical activity was restricted for at least ten days before the sweat test. No dietary restrictions were imposed. Sweat was induced thermally for 55 minutes in an environmental room with a temperature of 44° C. initially, 49° C. finally, and with a relative

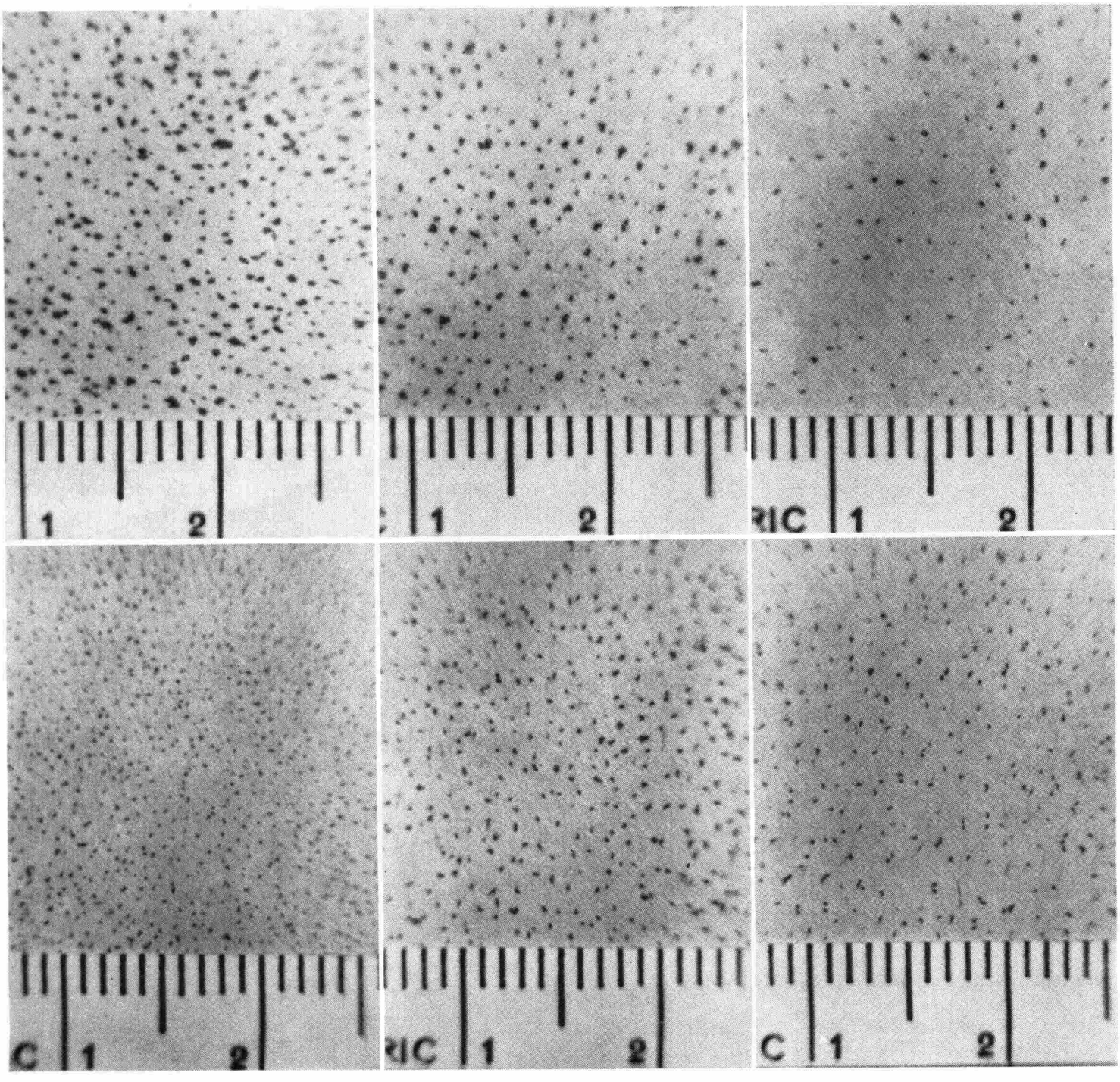

FIG. 1. Examples of sweat pore patterns for the two subjects, G. I. (upper) and F. Mc. (lower). The scale on the edge of each picture shows one centimeter. The left, forehead; the center, forearm; the right, back.

humidity of 80 to 90%. Various sweat rates were obtained by increasing the temperature, humidity and the amount of physical exercise on a treadmill. During the final 15 minutes of the test period each subject was subjected to what was considered by subjective impression of the experimenters to be a maximally tolerated stress of heat, humidity, and exercise. Most of the subjects showed the highest sweat rates at the 8th or 9th sweat collection period and further increases in room temperature, humidity and physical exercise failed to induce further increase in sweat rates. Three test sites were used in each subject; the center of the forehead, the suprascapular area of the back and the center of the volar aspect of the forearm. Aluminum chambers with an internal diameter of 2.4 cm, were secured with Weldwood® contact cement to the precleansed skin of the test sites. At time zero, subjects entered the environmental room and sweat was collected ten times on electrolyte-free filter papers within the aluminum chambers every five minutes after an initial ten minute period. Sweat pore patterns were obtained on starch iodine paper from the three test sites immediately after the final sweat collection. Examples of six such patterns from two subjects are shown in Figure 1. The number of active glands was determined by counting the black dots on the starch-iodine paper per cm^2 from various areas within each test site. At least five countings were made on each specimen and the results expressed as the mean value obtained. Sweat volume was determined by weighing the filter papers in an airtight plastic bottle immediately before and after each sweat collection.

Sweat was diluted with deionized water and was analyzed for its sodium content by flame photometry. The maximal free water clearance (FWC max) and the derived values for the sodium concentration of the precursor fluid were determined according to the model of Schwartz and Thaysen (11).

In most cases, the forehead produced the highest sweat rate and was thus the most suitable for calculation of the slope of the linear portion of the curve by the method of least squares. Only a few plots from the forearm became linear but in more than half the subjects, specimens from both the back and the forehead could be used for calculating the slope. Both areas gave approximately identical results. Because of this, specimens obtained from the forehead were used to calculate values for the sodium concentration of the precursor fluid in each subject except one (T.D.) in whom the back was used. Both maximal sweat rate (SR max) per gland (nl/min/gland) and FWC max per gland (nl/min/gland) were calcu-

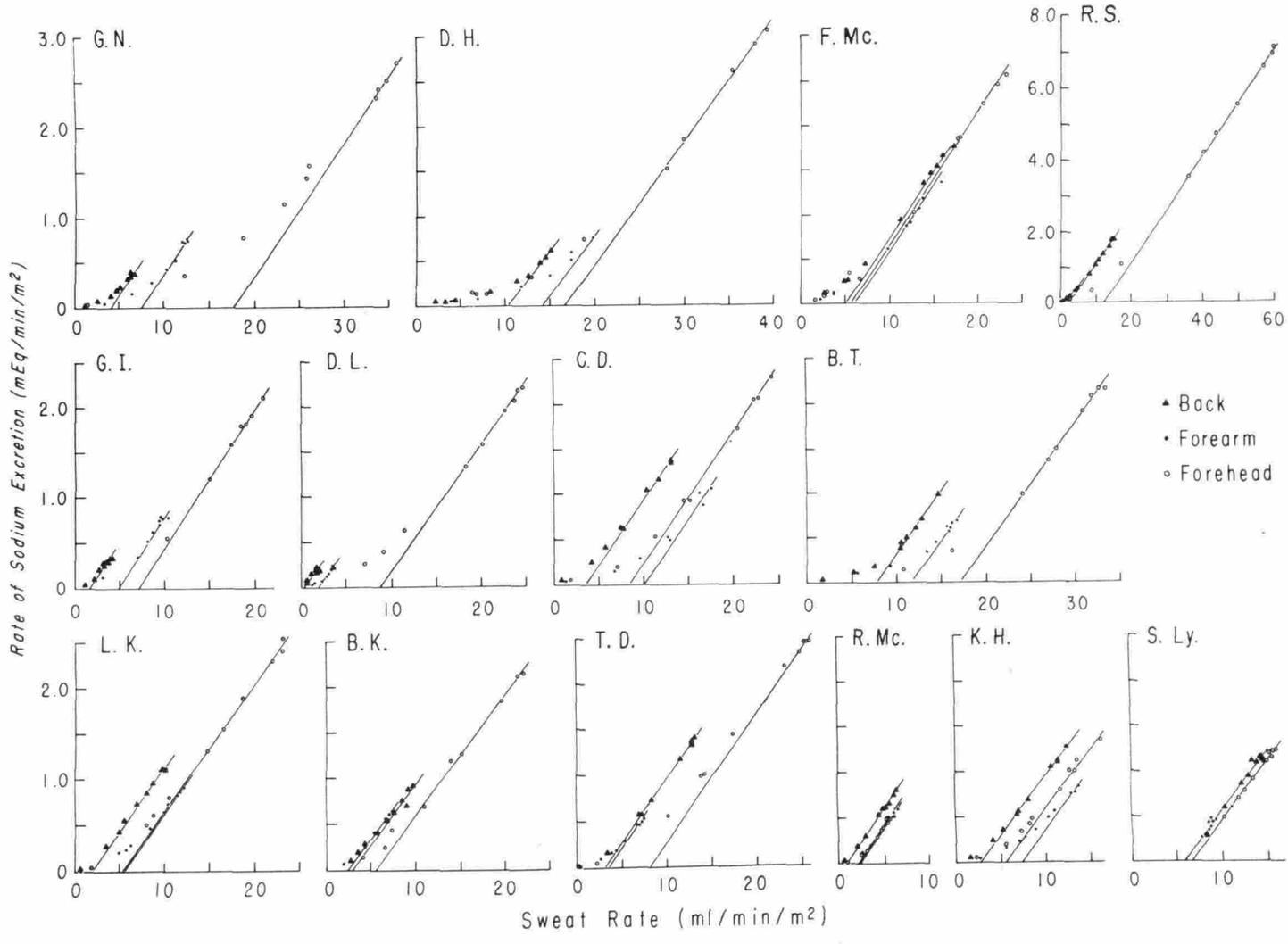

FIG. 2. The plots of sodium excretion rates vs. sweat rates for fourteen subjects. Note the differences in scale.

TABLE

Derived values for sodium concentration of the precursor fluid, number of active sweat glands, maximal sweat rates and maximal free water clearance

Subjects	Na concentration of the precursor fluid (mEq/L)	Forehead				
		Number of active sweat glands per cm²	FWC max (ml/min/m²)	SR max (ml/min/m²)	FWC max/gland (nl/min/gl)	SR max/gland (nl/min/gl)
1. B.T.	137	249	17.3	33.6	6.9	13.5
2. R.S.	147	189	12.0	59.5	6.3	31.5
3. R.Mc.	137	128	2.1	5.7	1.6	4.5
4. B.K.	130	111	5.5	22.1	5.0	20.0
5. L.K.	138	184	5.3	23.3	2.9	12.7
6. F.Mc.	149	233	5.8	23.1	2.5	9.9
7. S.L.	130	313	6.7	16.2	2.1	5.2
8. G.N.	148	120	18.0	36.0	15.0	30.0
9. C.O.	146	151	8.5	24.4	5.6	16.2
10. D.L.	139	196	8.9	24.8	4.5	12.7
11. D.H.	137	135	16.6	39.3	12.3	29.1
12. K.H.	133	157	5.8	16.4	3.7	10.4
13. G.I.	152	145	7.2	20.2	5.0	14.4
14. T.D.	140	218	8.2	26.0	3.8	11.9
Mean ± SE	140 ± 1.8	181 ± 14.5	9.1 ± 1.3	265. ± 3.2	5.5 ± 1.0	15.9 ± 2.3
		Forearm				
1. B.T.	137	176	11.8	16.8	6.7	9.5
2. R.S.	147	28	2.1	4.9	7.5	17.5
3. R.Mc.	137	136	2.3	6.7	1.7	4.9
4. B.K.	130	87	2.4	7.8	2.8	8.9
5. L.K.	138	145	5.5	12.2	3.8	8.4
6. F.Mc.	149	109	6.1	15.7	5.6	14.4
7. S.L.	130	151	5.7	11.3	3.8	7.5
8. G.N.	148	63	7.6	12.6	12.1	20.0
9. C.O.	146	101	10.1	17.8	10.0	17.6
10. D.L.	139	95	2.0	3.7	2.1	3.9
11. D.H.	137	121	14.1	19.8	11.7	16.4
12. K.H.	133	98	7.4	13.8	7.6	14.1
13. G.I.	152	97	5.0	10.5	5.2	10.8
14. T.D.	140	102	3.6	7.6	3.5	7.4
Mean ± SE	140 ± 1.8	108 ± 9.4	6.1 ± 0.9	11.5 ± 1.3	6.0 ± 0.8	11.5 ± 1.3
		Back				
1. B.T.	137	95	7.9	14.7	8.3	15.5
2. R.S.	147	51	2.5	14.8	5.0	29.0
3. R.Mc.	137	55	0.8	6.5	1.5	11.8
4. B.K.	130	51	2.9	9.8	5.7	19.4
5. L.K.	138	58	1.8	10.0	3.1	17.2
6. F.Mc.	149	77	5.2	17.2	6.8	22.3
7. S.L.	130	121	5.8	14.8	4.8	12.2
8. G.N.	148	37	4.1	6.6	11.1	17.8
9. C.O.	146	39	3.6	13.1	9.2	33.6
10. D.L.	139	49	0.4	2.0	0.8	4.1
11. D.H.	137	66	10.3	15.0	15.6	22.7
12. K.H.	133	58	2.7	12.5	4.6	21.5
13. G.I.	152	49	1.6	4.2	3.3	8.6
14. T.D.	140	85	3.2	13.1	3.8	15.3
Mean ± SE	140 ± 1.8	64 ± 5.9	3.8 ± 0.7	11.0 ± 1.2	6.0 ± 1.0	17.9 ± 2.0

FWC = Free water clearance; SR = Sweat rate; nl = nano liter (10^{-9} liter); SE = Standard error of the mean.

lated from the SR max per unit area (ml/min/m²) and FWC max per unit area (ml/min/m²) by dividing these factors by the number of active sweat glands in the corresponding test site.

RESULTS

Figure 2 shows plots of sodium secretion rates vs. sweat rates for the 14 subjects.

The Table lists the derived values for sodium concentration of the precursor fluid, the number of active sweat glands per cm², SR max and FWC max per unit area and per single gland for the three test sites in each subject. The average of the derived values for sodium concentration of the precursor fluid was 140 ± 1.8 mEq/L (SE) with a range of 130 to 152 mEq/L which is distinctly in the isotonic range. The number of the active sweat glands was highest on the forehead with an average of 181/cm² (range 111-313) and lowest on the back with an average of 64/cm² (range 37–121).

Both FWC max and SR max per m² and FWC max and SR max per gland showed a high individual variability in all test sites. Despite this variability as well as that in the population of active sweat glands, significant correlation was obtained between FWC max per m² and FWC

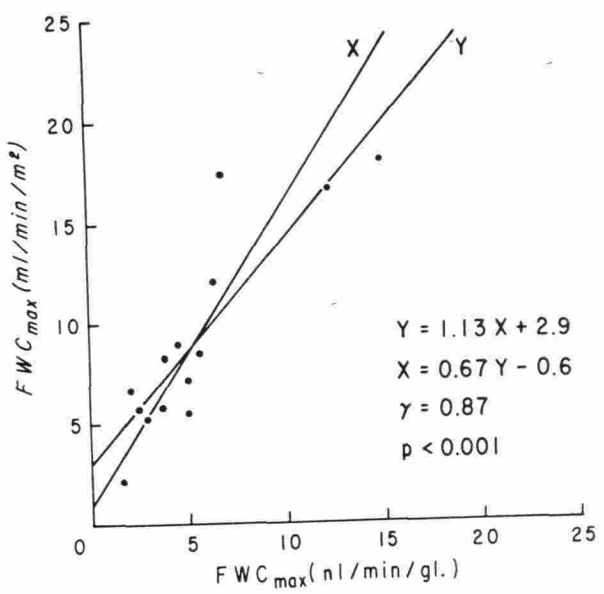

FIG. 3. Correlation between max FWC per m² and max FWC per gland, forehead. Both the regression of x on y and that of y on x are shown. The correlation coefficient is given as γ.

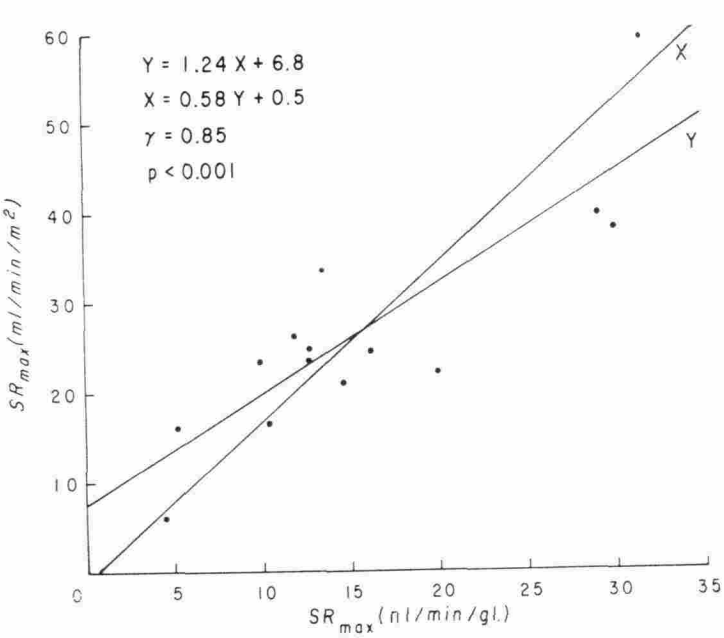

FIG. 4. Correlation between max SR per m² and max SR per gland, forehead.

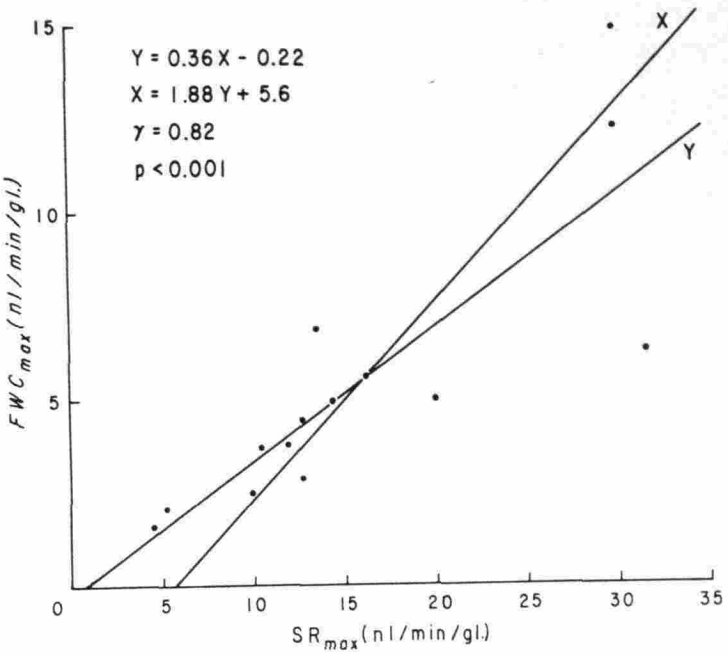

FIG. 5. Correlation between max FWC per gland and max SR per gland, forehead.

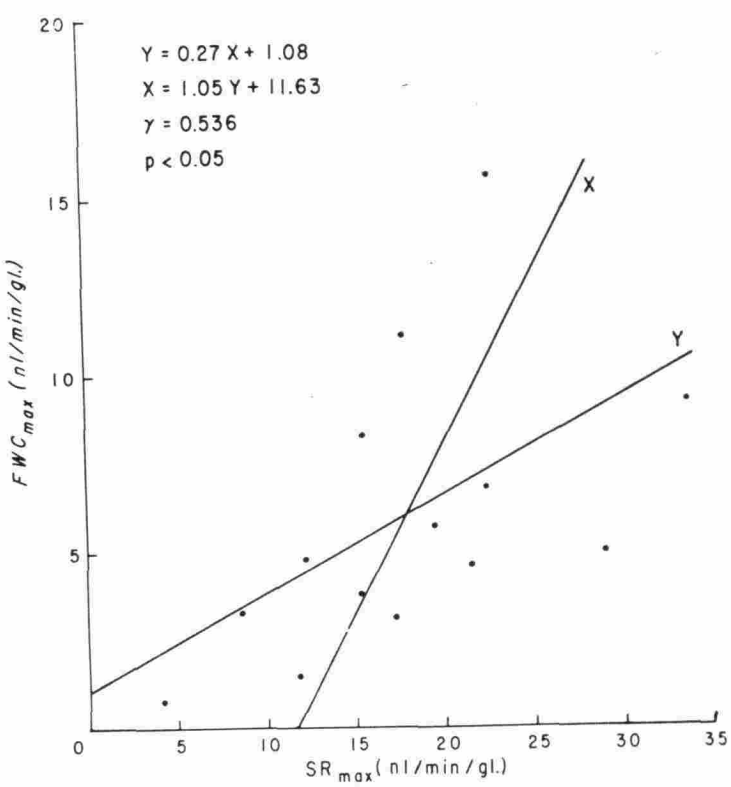

FIG. 6. Correlation between max FWC per gland and max SR per gland, back.

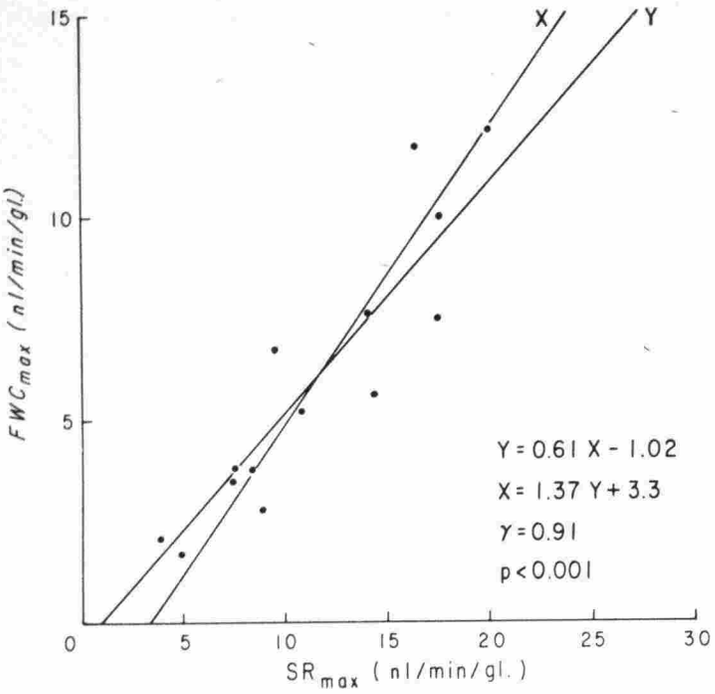

FIG. 7. Correlation between max FWC per gland and max SR per gland, forearm.

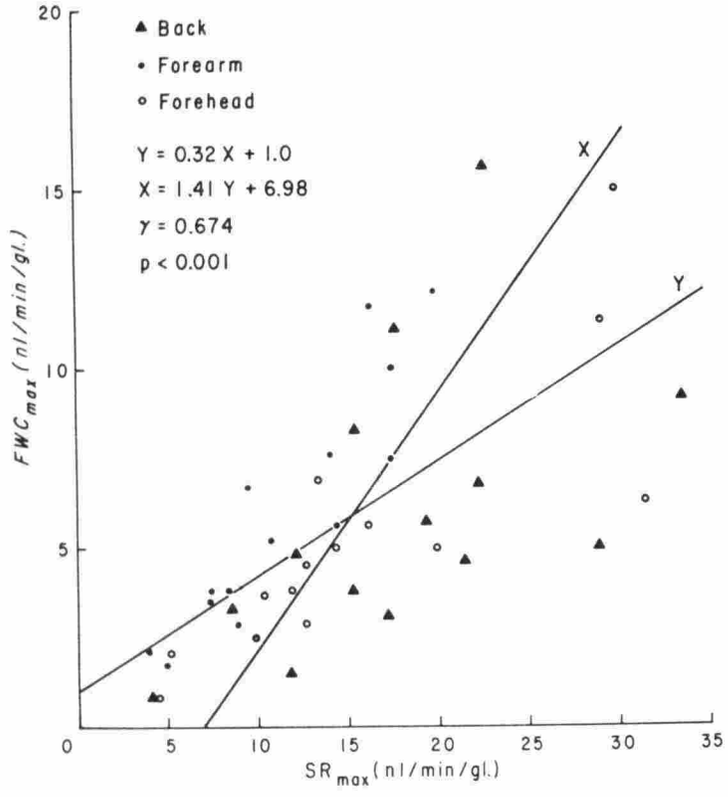

FIG. 8. Correlation between max FWC per gland and max SR per gland, for all test sites Each plot represents one subject.

max per gland and between SR max per m^2 and SR max per gland in each test site. The correlation plots obtained from the forehead are shown in Figures 3 and 4.

Figures 5, 6, 7 and 8 show the correlation between FWC max per gland and SR max per gland for forehead, back, forearm and for all test sites in all subjects. The highest correlation occurred on the forearm ($p < 0.001$) although every site showed a significant correlation. The regional relationships between FWC max per gland and SR max per gland for each subject is shown in Figures 9 and 10. Seven subjects (Fig. 9) suggest a correlation between FWC max per gland and SR max per gland, whereas the other seven subjects (Fig. 10) did not. Figures 9 and 10 also show that the individual variation in sweat gland function in terms of FWC per gland and the SR max per gland as expressed by the wide

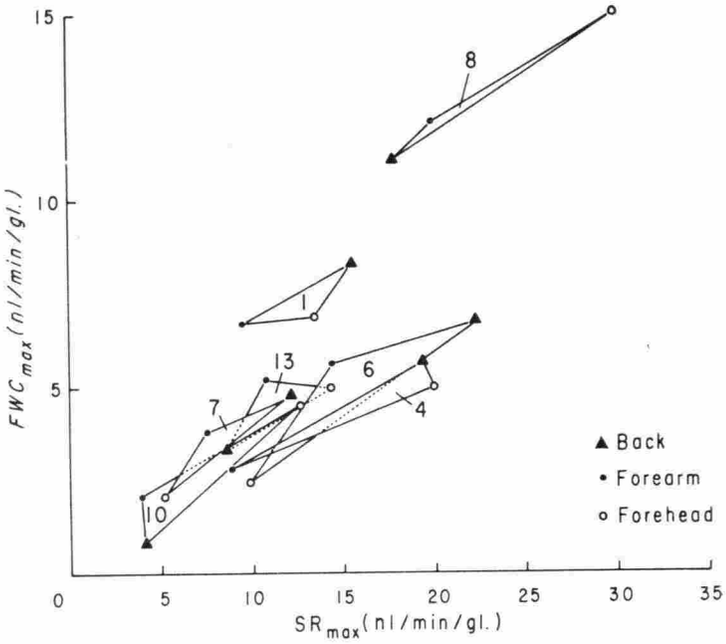

FIG. 9. Regional relationship between the max FWC per gland and the max SR per gland for 7 subjects who indicated a correlation between these factors. Each triangle represents one subject. The figure in each triangle corresponds to the subject number given in the Table.

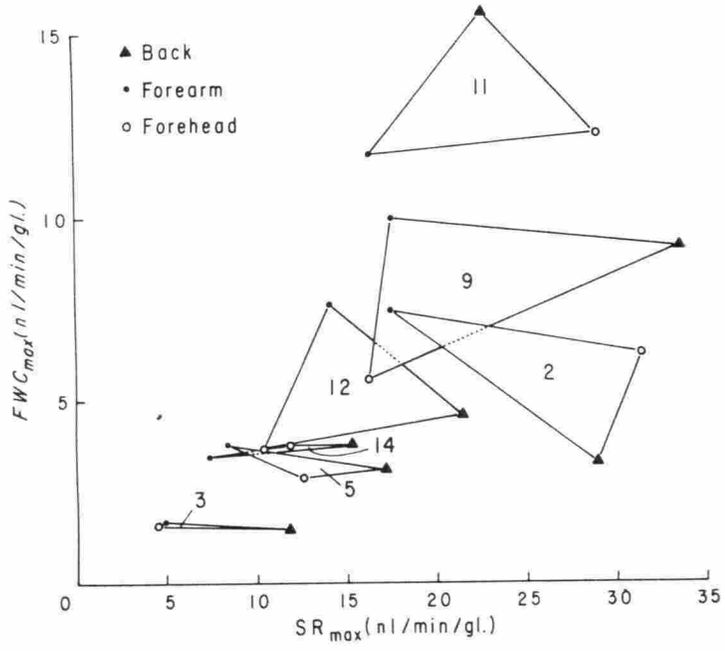

FIG. 10. Regional relationship between the max FWC per gland and the max SR per gland in the other seven subjects who showed no correlation between these two factors.

scatter of the triangles is greater than the regional variations as expressed by the size of each triangle.

DISCUSSION

Our data suggest that the great variation among individuals in eccrine secretory and reabsorptive capacity is largely dependent on differences in the function of the sweat glands, per se, rather than on a difference in the number of active sweat glands per unit area. However, in any given individual, regional variations are more likely to depend on differences in the number of sweat glands per unit area. Our data also demonstrate that in any given individual there is a significant correlation between FWC max per gland and SR max per gland. This indicates a possible functional correlation between the reabsorptive and secretory processes in the eccrine sweat gland which may be physiologically significant since a gland with a high capacity for both sweat secretion and sodium reabsorption would contribute more effectively to thermoregulation with a lesser tendency to produce sodium depletion. A sweat gland producing a low sweat sodium concentration and a high capacity to secrete may not be explained only by the effect of endogenous aldosterone since aldosterone suppresses sweat secretion and its effect is transient (7, 8).

The only possible factor which can produce an increase in both the secretory and reabsorptive capacity of the sweat glands may be sweat gland training, that is, an improvement in performance based on past repetitive sweating. Ohara (10) has reported that sweat rate and chloride reabsorption increase during the summer in persons living in a temperate zone. High sweat rates and low sweat chloride concentrations have also been noted in natives of the tropics (9). Thus, it is possible that the striking individual differences in sweat gland performance we observed could be the result of differing degrees of sweat gland training in our subjects.

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