Contribution of Leg and Splanchnic Free Fatty Acid (FFA) Kinetics to Postabsorptive FFA Flux in Men and Women

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We have previously shown that upper-body adipose tissue is more lipolytically active than lower-body adipose tissue in lean and obese women. The present studies were conducted to determine whether these regional differences are also present in men. Twenty-five lean, healthy men and 24 lean, healthy women underwent measures of body composition, postabsorptive systemic free fatty acid (FFA) flux, and leg and splanchnic FFA uptake and release. Upper-body adipose tissue was more lipolytically active than lower-body adipose tissue in both men (53.4 ± 32.2 *v* 26.6 ± 12.9 μmol · kg fat^{-1} · min^{-1}, $P < .001$, respectively) and women (41.2 ± 22.3 *v* 18.4 ± 8.2 μmol · kg fat^{-1} · min^{-1}, $P < .001$, respectively). The correlations between leg FFA release and systemic FFA flux were modest in women and men ($r = .38$, $P = .07$ and $r = .56$, $P = .003$, respectively) as were the correlations between splanchnic FFA release and systemic FFA flux ($r = .41$, $P = .06$ and $r = .40$, $P = .07$, respectively). No effect of gender on the relationship between leg or splanchnic FFA release and systemic FFA flux was detected. In summary, upper-body FFA release is greater than lower-body FFA release in both men and women, and the relationship between leg or splanchnic FFA release and systemic FFA release is weak and similar in men and women. These findings suggest that regional differences in postabsorptive FFA kinetics are unlikely to be responsible for differences in regional fat distribution.

BODY FAT DISTRIBUTION is an important predictor of the health consequences of obesity.[1] Indeed, fat distribution appears to be an important determinate of sex differences in serum lipid concentrations[2] and the insulin resistance of aging.[3] It has been suggested that differences in regional lipolytic rates may contribute to some of the adverse health effects of obesity via abnormally elevated free fatty acid (FFA) release.[1] However, the proximate factors that determine body fat distribution are unknown.

Sex steroids clearly have major effects on regional fat storage in humans. Whether these effects are mediated via changes in lipolysis, fatty acid storage, or both is uncertain. We previously reported that overnight postabsorptive FFA release from lower-body fat was significantly less than that from upper-body fat in lean and obese women.[4] This observation, combined with the findings of reduced meal fat uptake in lower-body fat of women,[5] suggested to us the possibility that regional differences in basal lipolysis could account for the predominately lower-body fat distribution in women compared with men. Unfortunately, no data are available to assess whether lower-body lipolysis is regulated differently than upper-body lipolysis in men and, if so, whether men and women differ in the relationship between systemic and regional (leg and splanchnic) FFA release.

The present studies were undertaken to address three issues. The first was to compare lipolytic rates of upper-body and lower-body adipose tissue (per kilogram fat) in men to assess whether the regional differences in FFA release[4] are unique to women. Because men have less lower-body fat than women, it was anticipated that lower-body lipolytic rates in men would be more similar to upper-body lipolytic rates. The second goal was to assess whether splanchnic FFA release is increased as a fraction of systemic FFA flux in men compared with women. Even lean men have greater amounts of visceral fat than lean women,[6] and thus an increased contribution of splanchnic lipolysis might be anticipated. Finally, if upper-body FFA release was greater than lower-body FFA release in both men and women, we wished to compare the relationship between regional FFA release and systemic FFA flux in men and in women. This would provide a more robust means of assessing whether there are sufficient gender-based variations in the regulation of postabsorptive regional lipolysis to account for the differences in regional fat distribution between men and women.

SUBJECTS AND METHODS

Subjects

Informed written consent was obtained from 25 non-obese men and 24 non-obese, premenopausal female volunteers. All subjects were in good health, were not taking any medication, and had maintained a stable weight for more than 2 months before the studies. A summary of subject characteristics is provided in Table 1.

Materials and Methods

The [9,10^{3}H]palmitate and [9,10^{3}H]oleate used in these studies were obtained from NEN Research Products (North Billerica, MA). Indocyanine green (Cardio-Green) was purchased from Becton Dickinson (Cockeysville, MD).

Plasma palmitate, oleate, and total FFA concentrations and palmitate or oleate specific activity (SA) were determined by a modification[7] of a previously reported HPLC technique,[8] using [^{2}H$_{31}$]palmitate as an internal standard. A quality-control sample was run with each assay to ensure minimal (<3%) interassay variation for FFA concentration and SA.

Body fat and fat-free mass, as well as leg fat, were measured using dual-energy x-ray absorptiometry (Lunar Radiation, Madison, WI).[9] Regional fat mass was determined using the appropriate program in the Lunar software version 3.4. Upper-body fat was determined by subtracting leg fat (both legs) from total body fat.[4] Plasma indocyanine green concentrations were measured using a spectrophotometer on the day of the study, using precautions as previously described.[4]

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Table 1. Subject Characteristics

Characteristic	Women (n = 24)	Men (n = 25)
Age (yr)	29 ± 7	28 ± 8
Height (cm)	165 ± 7	180 ± 8
Weight (kg)	61.4 ± 7.2	77.5 ± 9.0
Body fat (kg)	18.2 ± 5.0	13.5 ± 4.1
Leg fat (kg)	3.6 ± 1.0	2.1 ± 0.7
Leg/body fat (%)	40 ± 4	31 ± 4

NOTE. Values are the mean ± 1 SD. With the exception of age, all variables are significantly different ($P < .01$) between men and women. Leg/body fat refers to the percent of total body fat present in both legs as assessed by dual-energy X-ray absorptiometry.

Protocol

Each subject consumed all meals as provided by the Mayo Clinic General Clinical Research Center (GCRC) for a minimum of 3 days before the study. The diets provided 40% of energy intake as fat, 40% as carbohydrate, and 20% as protein. Energy intake was allowed to vary slightly from an isoenergetic diet in one third of the volunteers to increase the range of interindividual differences in postabsorptive FFA flux. Each participant was admitted to the GCRC the evening before the study, and an 18-gauge infusion catheter was placed in a forearm vein and infused with 0.45% NaCl at 20 mL/h. Blood was sampled before starting the indocyanine green infusion to be used for construction of the indocyanine green calibration curve and as background for FFA specific activity.

The morning of the study, the subjects were transferred to the Vascular Radiology Laboratory, where a 5F, Terumo sheath was introduced into the right femoral artery using standard percutaneous technique. A 20-cm long, 4F straight catheter with six distally placed side holes (special order; Cook, Bloomington, IN) was placed through the sheath with the catheter tip in the common iliac artery. This catheter was used for arterial blood sampling, and the sheath was used to infuse indocyanine green. The right femoral vein was then punctured in a similar manner and a 6F Terumo sheath was introduced. The distal tip of the sheath was placed in the external iliac vein a few centimeters above the inguinal ligament and was used to sample blood draining the right leg. A 5F Simmons II catheter (Cook) with four distal side holes was placed through the sheath, and the catheter tip was placed in the right hepatic vein to sample blood draining the splanchnic bed. Catheter position was confirmed with injection of approximately 5 mL iodinated contrast material. A solution of 0.45% NaCl was infused through the sheaths and catheters to maintain patency. The volunteers were then transferred back to the GCRC for completion of the study.

After being transferred back to the GCRC, the subjects rested in bed for the remainder of the study. An infusion of [9,10^{3}H]palmitate 0.3 μCi/min (n = 8 men and 8 women) or [9,10^{3}H]oleate 0.3 μCi/min (17 men and 16 women) was begun through the forearm vein infusion catheter upon returning to the GCRC. To allow measurement of leg and splanchnic plasma flow, a primed, constant infusion of indocyanine green was begun at the same time as the FFA tracer. After allowing 30 minutes for isotopic equilibration, arterial, femoral venous, and hepatic venous blood samples were taken at 15-minute intervals over 30 to 45 minutes. Following completion of the study, all catheters were removed and local hemostasis was obtained. The subjects remained in the hospital under observation until the following morning. Some of the volunteers underwent these measurements as part of other studies of FFA metabolism.[10,11]

Calculations

Leg[12] and splanchnic[13] plasma flow were calculated as previously described. Systemic total oleate or palmitate flux was calculated from the arterial steady-state [^{3}H]oleate or [^{3}H]palmitate SA and extrapolated to total FFA flux.[14] Because plasma FFA concentrations and SA were constant over the sampling interval, as was splanchnic and leg plasma flow, steady-state plasma FFA concentrations and SA were used together with measures of leg and hepatic plasma flow to measure regional (leg and splanchnic) FFA uptake and release.[4] FFA release per kilogram leg fat and per kilogram upper-body fat was calculated as previously described.[4] Upper-body nonsplanchnic FFA release was calculated using the formula: nonsplanchnic upper-body FFA release = FFA flux − [(leg FFA release ×2) + splanchnic FFA release].

Statistics

All results are expressed as the mean ± 1 SD. Comparisons of data for subject characteristics between men and women were made using a nonpaired t test. Comparisons of leg adipose tissue FFA release and upper-body adipose tissue FFA release (per kilogram fat) were made using a paired t test. To assess the relationship between leg and splanchnic FFA kinetics and systemic FFA flux, a linear regression analysis was performed using regional FFA uptake or release values as dependent variables and systemic FFA flux values as independent variables. A review of the scatter diagram suggested a leveraging effect from outlier values in the analysis of leg and splanchnic FFA release in men and women. The Spearman rank correlation coefficient was therefore used because it is resistant to the influence of outlier values and non-normal distribution. The Pearson correlation coefficient was used to analyze the relationship between regional FFA uptake and FFA flux. To determine whether there were differences in the relationship between regional FFA uptake and release and systemic FFA flux in men versus women, regional FFA uptake or release values were included as dependent variables in multiple linear regression analysis using systemic FFA flux, gender, and a gender-by-FFA flux interaction as independent variables.

RESULTS

Subject Characteristics

Men participating in this study were significantly taller and heavier than the women, with less body fat, less leg fat, and a lower percentage of leg fat as body fat (Table 1). The hepatic vein catheter could not be placed in two women and three men; therefore, splanchnic FFA kinetic data are available for 22 women and 22 men.

FFA Release

Steady-state postabsorptive FFA flux was 553 ± 233 μmol/min (range, 207 to 1,090) in women and 548 ± 222 μmol/min (range, 219–1,010) in men.

The simultaneous leg FFA release rates in women were 64 ± 30 μmol/min (range, 23 to 147). In men, leg FFA release was 54 ± 23 μmol/min (range, 18 to 101). Release of FFA from the adipose tissue of one leg accounted for 13% ± 6% of total FFA flux in women and 10% ± 4% of FFA flux in men ($P = .10$, men v women).

Spearman rank correlations between leg FFA release and systemic FFA flux for women and men were .38 ($P = .07$) and .56 ($P = .003$), respectively (Fig 1). The relationships between leg FFA release and systemic FFA

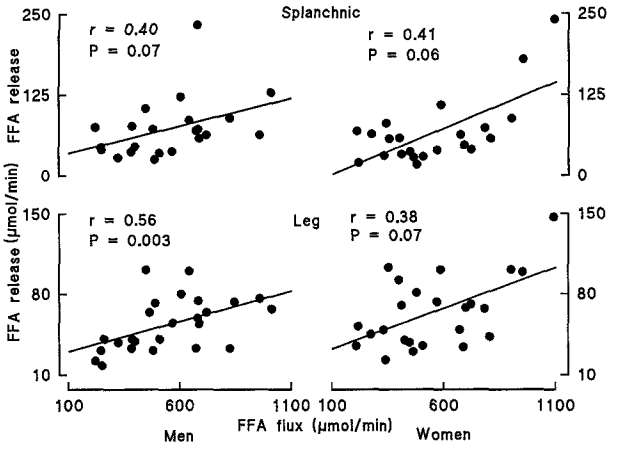

Fig 1. Leg and splanchnic FFA release rates plotted versus systemic FFA flux in men and women. Spearman rank correlation coefficients are shown.

flux were not different between men and women, as assessed by multiple linear regression analysis either with or without the outlier values. The correlation between leg FFA release and systemic FFA flux for men and women combined was statistically significant ($r = .31, P = .001$).

Basal splanchnic FFA release was 66 ± 52 μmol/min in women (range, 17 to 241), providing 13% ± 8% of systemic FFA rate of appearance. In men, splanchnic FFA release was 73 ± 46 μmol/min (range, 28 to 233), representing 14% ± 8% of systemic FFA flux (P = NS, men v women).

Spearman rank correlation coefficients between splanchnic FFA release and systemic FFA flux in women and men were .41 ($P = .06$) and .40 ($P = .07$), respectively (Fig 1). As assessed by multiple linear regression analysis, there was no effect of gender on the relationship between splanchnic FFA release and systemic FFA flux (with or without outlier values), although there was a significant correlation ($r = .32$, $P = .001$) between the two variables for the combined groups.

Upper-body adipose tissue FFA release was 424 ± 206 μmol/min (range, 111 to 796) in women and 444 ± 203 μmol/min (range, 176–876) in men. Upper-body adipose tissue FFA release in women was greater ($P < .001$) than lower-body adipose tissue FFA release (41.2 ± 22.3 v 18.4 ± 8.2 μmol · kg fat^{-1} · min^{-1}). In men, upper-body adipose tissue FFA release was also greater ($P < .001$) than lower-body FFA release (53.4 ± 32.2 v 26.6 ± 12.9 μmol · kg fat^{-1} · min^{-1}, respectively).

For subjects in whom splanchnic FFA release data was available, upper-body nonsplanchnic FFA release was calculated. Upper-body nonsplanchnic FFA release was 356 ± 190 μmol/min in women (range, 67 to 661) and 374 ± 188 μmol/min in men (range, 100 to 740), accounting for 61% ± 17% and 66% ± 13% of systemic FFA flux in women and men, respectively (P = NS, men v women).

FFA Uptake

Leg FFA uptake in women was 40 ± 23 μmol/min (range, 13 to 95), representing 8% ± 5% of systemic FFA uptake. In men, leg FFA uptake was 54 ± 23 μmol/min (range, 18 to 101), accounting for 7% ± 2% of FFA uptake. There was a significant correlation between leg FFA uptake and systemic FFA flux (Fig 2) in both women and men ($r = .45, P = .03$ and $r = .80, P < .001$, respectively). Multiple regression analysis confirmed a significant ($P < .005$) association between leg FFA uptake and FFA flux in the combined group of men and women, but no effect of gender on this relationship was detected.

Splanchnic FFA uptake was 165 ± 64 μmol/min (range, 29 to 316) in women, accounting for 34% ± 15% of systemic FFA uptake. In men, splanchnic uptake was 184 ± 91 μmol/min (range, 65 to 401), accounting for 35% ± 19% of systemic FFA flux (P = NS v women). Splanchnic FFA uptake was highly correlated with FFA flux in women ($r = .52, P = .01$) and in men ($r = .61, P = .003$). Multiple linear regression analysis confirmed the association between splanchnic FFA uptake and FFA flux ($P < .05$), but no effect of gender on this relationship was detected.

DISCUSSION

The present studies were conducted as part of ongoing investigations to examine the potential role of regional differences in adipose tissue lipolysis in determining body fat distribution in humans. Overnight postabsorptive FFA flux and leg and splanchnic FFA uptake and release were measured in lean, healthy men and women. Upper-body adipose tissue FFA release was significantly greater than lower-body FFA release relative to fat mass in both men and women. Although correlations were found between systemic FFA flux and regional FFA release, the associations were weak and unaffected by gender. These findings strongly support the concept of regional heterogeneity of adipose tissue lipolysis in adult humans, but suggest that regional differences in postabsorptive lipolytic rates are not a major reason for differences in body fat distribution between men and women.

The failure to find strong associations between systemic FFA flux and leg or splanchnic FFA release is most likely due to regional differences in the regulation of adipose tissue lipolysis. However, problems with the experimental

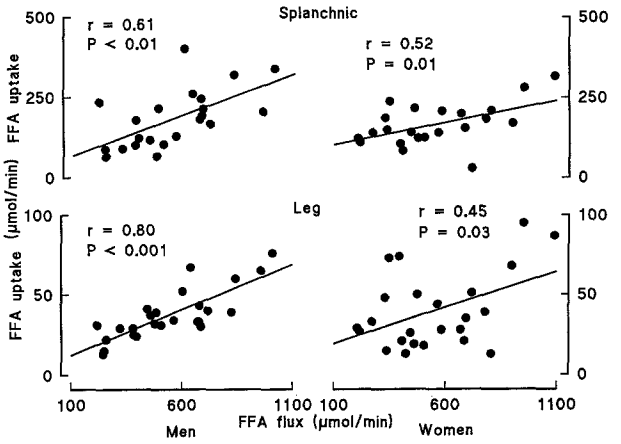

Fig 2. Leg and splanchnic FFA uptake rates plotted versus systemic FFA flux in men and women. Pearson correlation coefficients are shown.

design and methodologic errors must be considered as alternative explanations. We included individuals with a wide (fivefold) range of basal FFA flux to optimize the evaluation of this relationship. Thus, the experimental design seems appropriate to detect strong associations if they exist. Isotope dilution techniques provide accurate measures of systemic FFA flux,[7,8] and the HPLC assay of plasma FFA concentration and SA is highly precise (coefficient of variation for replicate analysis, 3% to 4%).[8] The inclusion of a quality-control sample with each analytical run ensured that the interassay variation of the standard curves was kept to less than 3% to 5%. Leg plasma flow measurement by intraarterial indocyanine green infusion under basal conditions is precise, with a coefficient of variation for baseline plasma flow of 6% ± 1%.[15] The indocyanine green infusion technique for predicting splanchnic plasma flow provides accurate results when compared with independent techniques such as Doppler flow probes.[16] It therefore seems unlikely that the weak association between regional FFA release and systemic FFA flux can be attributed primarily to imprecise plasma flow or FFA measurement techniques. In support of this conclusion, correlations between regional FFA uptake and systemic FFA flux were substantially better than correlations between regional FFA release and systemic FFA flux; regional FFA uptake and release calculations use the same variables. Measurement error would be expected to affect regional uptake and release data equally.

The present study confirms the finding that upper-body lipolysis is greater than lower-body lipolysis in women,[4] and extends it to men. Several in vitro studies have documented that basal lipolytic rates of lower-body fat cells are greater than or equal to rates of upper-body fat cells.[17-19] The reason for the discrepancies between in vitro and in vivo findings is not immediately clear, but several explanations should be considered. It is possible that ambient circulating insulin concentrations in the postabsorptive state have different suppressive effects on upper-body and lower-body fat cells in vivo, such that lower-body adipocytes are relatively more suppressed. It is also possible that circulating and local catecholamine availability interacts with the differences in β- and α_2-adrenoceptor responsiveness between adipose tissue depots[20-23] to selectively stimulate upper-body adipocytes. Finally, growth hormone is a known regulator of lipolysis[24] and might preferentially stimulate lipolysis in upper-body fat cells. Additional in vivo studies will be necessary to assess these possibilities.

The reduced FFA release from lower-body fat (relative to upper-body fat) in women[4] suggested to us that this could be a mechanism for the preferential accumulation of lower-body fat. The finding of similar differences in men implies that this is not the case. Recent studies by Mårin et al have documented a lower storage of meal fat in lower-body fat in women[5] and men.[25] This reduced storage appears to be combined with an appropriately reduced FFA release, allowing an eventual equilibration between fatty acid storage and release. The finding that regional lipolysis relates to systemic lipolysis in a similar manner in postabsorptive men and women implies that differences in fatty acid storage, not basal lipolysis, may be a significant contributor to gender differences in body fat distribution. However, it remains possible that regional differences in lipolysis after meal consumption[10] or during exercise contribute to gender-based differences in body fat distribution.

The finding of only a weak correlation between splanchnic FFA release and systemic FFA flux is not completely unexpected. Some FFAs released into the portal circulation by omental and mesenteric adipose tissue undergo first-pass hepatic extraction[26] and thus never enter the systemic circulation. The liver therefore acts as a buffer between visceral adipose tissue lipolysis and systemic FFA availability. This effect could obscure any relationship between factors that stimulate systemic and visceral lipolysis.

Leg FFA release contributed only a small portion of systemic FFA release in both men and women, and the relationship between leg and splanchnic FFA release and systemic FFA release was weak in both groups. This implies that a majority of the variation in systemic FFA availability is contributed by nonsplanchnic (subcutaneous) upper-body adipose tissue. It is likely that this adipose tissue depot is more responsive to factors that regulate basal FFA availability, and therefore variations in FFA release from this tissue bed account for the majority of the variation in overnight postabsorptive FFA flux. This may not be true after meal consumption[10] or under conditions of catecholamine-stimulated lipolysis.[11]

Of note is the disassociation between regional FFA uptake and release. Leg FFA uptake in women was less than FFA release, whereas the two values were approximately equal in men. This may relate to the increase in leg muscle mass in men, which would necessitate greater FFA uptake to meet lipid oxidative fuel needs. Leg adipose tissue, being regulated separately and with a separate circulatory system from muscle, would release FFA at a rate independent of leg FFA uptake. A similar disassociation between net splanchnic FFA release and splanchnic FFA uptake is apparent in both men and women.

In summary, the relationship between leg and splanchnic FFA release and systemic FFA flux in lean, healthy men and women was surprisingly similar. Although there were significant regional differences in adipose tissue lipolytic rates, men and women were similar in this regard. Both groups had reduced FFA release from lower-body adipose tissue versus upper-body adipose tissue. These findings suggest that regional differences in overnight postabsorptive lipolysis do not contribute substantially to regional differences in body fat distribution in men and women. A better understanding of the mechanisms through which preferential body fat accumulation occurs in specific regions will require studies of both FFA uptake and release under appropriate circumstances.

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