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Chronic undernutrition and metabolic adaptation

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An adaptive response is an inevitable consequence of sustained perturbation in the environment. This adaptive response may be of three kinds: (a) biological or genetic, (b) physiological or metabolic and (c) behavioural or social. They are not completely separate entities as they interact with each other at several levels. Adaptive changes are not without cost. The process and the costs involved may be: (a) overt or covert, (b) reversible or irreversible and (c) transient or permanent. Every adaptation has its cost and there is no such thing as a 'costless' adaptation. An adaptive response may compromise function and performance in order to further the survival of the individual. Adaptation is a relatively slow process and should be distinguished from the rapid regulatory role of homeostatic mechanisms.

Over the last two decades, it has been suggested that the energy metabolism of individuals is more variable and adaptable than previously believed and that allowances need to be made for this when arriving at estimates of human energy requirements. Several important publications have drawn attention to the possibility of such physiological variability in energy utilization between individuals (Durnin *et al.* 1973; Edmundson, 1980) and within individuals (Sukhatme & Margen, 1982). Norgan (1983) has critically evaluated the fourfold evidences that have been adduced for this variation and adaptation in energy metabolism:

- (1) in any group of 20 or more similar individuals, energy intake can vary as much as two-fold (Widdowson, 1962);
- (2) large numbers of apparently healthy active adults exist on lower than required energy intakes (Durnin, 1979);
- (3) the efficiency of work and work output per unit energy intake is variable (Edmundson, 1979);
- (4) observations based on studies of experimental or therapeutic semi-starvation (Keys *et al.* 1950; Apfelbaum, 1978) and overfeeding of humans (Sims, 1976; Norgan & Durnin, 1980) support this.

Although differences in body size and levels of physical activity may provide explanations for some or most of these observations, what is implied or explicitly stated is that metabolic efficiency and mechanical work efficiency of the individuals are variable and show an adaptation to varying levels of energy intake (Norgan, 1983). These same observations on low intakes in adults (Durnin, 1979), increased work efficiency

(Edmundson, 1979) and following experimental semi-starvation (Keys *et al.* 1950) constitute the important biological arguments for metabolic adaptation and an enhanced metabolic efficiency in chronic undernutrition.

When there is a sustained reduction in energy intake, changes in body composition and energy expenditure will occur in order to attain a new, but lower level of energy balance. When energy intake is reduced, the total energy expenditure (TEE) will also be reduced. TEE is conventionally considered to be made up of three components: (1) basal metabolic rate (BMR) which accounts for between 60 and 75% of the daily TEE; (2) physical activity, the second component whose contribution to TEE will depend both on its duration and intensity and (3) thermogenesis which is defined as the energy expenditure above BMR and physical activity and includes the effects of food intake, cold exposure, thermogenic agents and stress.

Ferro-Luzzi (1985) summarized our current thinking on the ways in which an individual may respond to sustained energy imbalance by metabolic adaptation which represents a complex integration of several different processes that occur during energy deficiency. These processes are expected to occur in a phased manner which then results in a new equilibrium at the lower level of energy intake. Individuals who have gone through the adaptive processes that occur during this long-term energy deficiency exhibit more or less permanent sequelae or costs of adaptation, which include a smaller stature and body size, altered body composition, a lower BMR and a diminished level of physical activity with the possibility of an enhanced metabolic efficiency of energy handling by the active tissues of the body. The objective of the present paper is to critically re-examine the existence of mechanisms which may contribute to any apparent metabolic efficiency of the tissues that may influence the contributions from the three physiological components of TEE in the chronically energy-deficient (CED) or undernourished adult.

BASAL METABOLIC RATES IN CHRONIC UNDERNUTRITION

Metabolic efficiency in basal metabolism

It is universally assumed that the physiological and metabolic responses of the human body to CED are similar to, and can be explained on the basis of, the changes that occur during experimental or therapeutic semi-starvation. As a result, there is considerable interest in seeking physiological changes suggestive of an increase in the metabolic efficiency of the active tissues even in CED subjects. A reduction in O₂ consumption per unit active tissue has been considered indicative of enhanced metabolic efficiency (Grande, 1964) and as a definitive index of the existence of metabolic adaptation in BMR (Waterlow, 1986). A decrease in BMR per kg fat-free mass (FFM) or lean body mass (LBM) implies that the increase in metabolic efficiency is demonstrable in the other components of energy expenditure, particularly a decrease in the energy cost of physical activity of an individual (Ferro-Luzzi, 1985).

BMR expressed either in absolute terms or expressed per unit body surface area (BSA) have always been found to be lower in chronically undernourished subjects. This was true of German prisoners of war, victims of severe malnutrition in ghettos, chronically malnourished adults studied during the war and malnourished or starved individuals seen during natural disasters such as famine. Many of the previously mentioned studies on malnourished subjects were, in fact, interpreted as failing to

demonstrate any significant decrease in metabolic rate per kg FFM, although the BMR per unit BSA were definitely lower (Beattie & Herbert, 1947; Venkatachalam *et al.* 1954). Ashworth (1968), while reporting a 12% reduction in BMR in Jamaican subjects on low energy intakes, also confirmed her inability to show evidence of enhanced metabolic efficiency in BMR. These observations in the undernourished are in marked contrast to the invariable and constant demonstration of a decrease in BMR per kg active tissues seen during experimental semi-starvation in humans (Grande, 1964).

More recently, BMR measurements made in apparently healthy, but undernourished, labourers showed a definite reduction in the metabolic activity of the LBM which could perhaps be interpreted as an enhanced metabolic efficiency, although the major share of the fall in BMR was attributable to a decrease in the total mass of active tissues (Shetty, 1984). Recalculation of data from an earlier report by Ramanamurthy *et al.* (1962) also showed a lowering of BMR per kg FFM in adult, undernourished males. However, a large number of measurements made, over the last decade, in CED subjects do not confirm the existence of an enhanced metabolic efficiency as indicated by a reduced O₂ consumption per unit FFM (Soares & Shetty, 1991). On the contrary, it has now been observed that the BMR expressed per kg FFM was significantly higher in CED subjects than in well-nourished controls. This large group of healthy, CED subjects had short statures, low body weights, low FFM and low body mass indices (weight/height²; BMI <18). They had low energy intakes, came from poorer socio-economic groups and were urban or rural labourers. A comparable and equally large series of BMR measurements reported by Srikantia (1985), also in males from lower socio-economic status, showed a similar trend; BMR per unit body weight increased as the weight-for-height, expressed as a percentage of standard values, diminished. Recent BMR measurements made in rural South India by McNeill *et al.* (1987) were also comparable with those obtained both by Srikantia (1985) and by Soares & Shetty (1991). Results of these three studies with large sample sizes also provided no evidence of metabolic adaptation in individuals from poor socio-economic groups on lower planes of energy intake. Since expressing BMR per kg FFM is aimed at correcting for differences, in body sizes of groups of individuals, it is necessary to eliminate the possible mathematical artefacts by analysis of covariance (Ravussin & Bogardus, 1989). Thus, it has been shown that subjects with CED have a lower BMR when adjusted for body weight or FFM implying that there may indeed be some covert metabolic economy in the active tissues even if the expression BMR per kg FFM fails to reveal this overtly (Soares & Shetty, 1991). However, since whole-body protein turnover has been estimated to contribute as much as 30% of BMR (Jackson, 1985), the lack of any reduction in protein synthesis rates in these CED individuals (Soares *et al.* 1991) indirectly supports the suggestion that the metabolic activity of the FFM is unlikely to be reduced in chronic undernutrition.

An objective assessment of all the data accumulated over the last 30 or more years leads to two definite conclusions: (1) the BMR of undernourished subjects, on an absolute basis (MJ/d) is significantly lower than the well-nourished and this is largely accounted for by the low body weights of these individuals; (2) the reduced metabolic rate per unit FFM, considered hitherto as an expression of enhanced metabolic efficiency in the undernourished in earlier studies of the 1960s (Ramanamurthy *et al.* 1962) and 1970s (Shetty, 1984), is not evident in the more recent BMR measurements made over the last decade in individuals with more or less similar anthropometric characteristics, except when statistically adjusted for differences in FFM. The changes in BMR observed

in chronically undernourished individuals over the last two to three decades in India, thus, seems to show a secular trend occurring over a period of time when food intake surveys have also indicated a remarkable increase in the mean energy intakes of individuals and households (Rao *et al.* 1986).

The evidence that mechanisms of improved efficiency of energy utilization are operative in free-living populations on low energy intakes but compromised anthropometry, thus, appears to be tenuous and contradictory. If enhanced metabolic efficiency is indeed present during chronic undernutrition, then a reduction in BMR per kg FFM may not necessarily reflect this phenomenon. Either BMR per kg FFM is not an index of metabolic efficiency as is universally believed (Waterlow, 1986), or metabolic efficiency is neither a characteristic nor a constant feature of chronic undernutrition. A reduction in BMR per unit FFM is perhaps not *sine qua non* for metabolic efficiency. One possible way in which these apparently contradictory findings may be rationalized is to seek alternative explanations based on the changes in body composition seen in chronic undernutrition.

BMR and its relationship to body composition in chronic undernutrition

Lawrence *et al.* (1988) observed differences in BMR between Scottish, Gambian and Thai women which could largely be explained in terms of the differences in the FFM, since individuals in all the three groups with similar FFM had similar BMR. Thus, differences between the groups in BMR per kg FFM were largely explained by the between-group differences in the FFM. Within any of the groups, the BMR per kg FFM decreased as the body weight or FFM increased. Lawrence *et al.* (1988) suggested that variations in BMR per kg FFM between the heavy and light individuals in any group could indicate that the composition of the FFM was not constant. Owen *et al.* (1990) and Weinsier *et al.* (1992) respectively have shown that BMR per kg body weight and per kg FFM fall as body weight or FFM increases. Weinsier *et al.* (1992) have indicated that the index BMR/FFM does not take into account the fact that the BMR of FFM is not constant over a wide range of FFM and that the relative proportions of its metabolic components may change as FFM changes. In the Minnesota semi-starvation studies, at the end of 24 weeks, muscle losses were estimated at 41% whereas the reduction in FFM was only 27% (Grande, 1964); a situation quite unlike the changes seen in acute starvation in humans. Studies examining changes in body composition of adults with naturally evolving chronic undernutrition revealed a gradation of changes related to the severity of the deficiency (Barac-Nieto *et al.* 1978). Body cell mass (i.e. cell solids and intracellular water estimated from total body water and extracellular water) was reduced even with moderate deficiency and the muscle mass was more affected than other cells; muscle cell mass seemed to decrease linearly with the increasing severity of undernutrition, while the visceral cell mass showed little change. Body fat and body cell mass reduced by 29% while muscle cell mass decreased by 41% in severe undernutrition. Estimates of body composition in CED subjects made by creatinine excretion also indicate a greater reduction in muscle mass with visceral mass apparently being spared (Soares *et al.* 1991). The visceral component of the FFM (liver, heart, kidney) has been estimated to utilize nearly 45% of the total O₂ consumption at rest while skeletal muscle which comprises up to 50% of the body weight contributes only 18% to the resting metabolic rate (Passmore & Draper, 1965). The combined weight of the brain and liver

which accounts for 3–5% of the total body weight, utilizes as much as 40% of resting O_2 consumption (Keys *et al.* 1973). Elia (1992) has estimated that 40% of the body weight of an adult man is muscle, but contributes to only 22% of BMR. The contributions of organ mass (OM) to FFM has been shown to be related to FFM; OM:FFM increasing as FFM reduces in both males and females (Garby & Lammert, 1992). Thus, if the FFM (or LBM) had a significantly greater proportion of the metabolically active visceral mass and a reduction in the mass of the relatively less active muscle, then BMR expressed per kg FFM would be high. This may indeed be the case with mild to moderate energy deficiency since muscle mass is more likely to be reduced than non-muscle or visceral mass. As undernutrition progresses, mobilization of tissues from the visceral mass occurs in the more severe forms of energy deficiency, resulting in the BMR per kg FFM being reduced. Along with these changes in body composition seen during long-term energy inadequacy, there is also a change in the extracellular fluid compartment which will also influence the BMR expressed per unit active tissue (Barac-Nieto *et al.* 1978; Widdowson, 1985). Chronically undernourished subjects who have to do hard physical labour may have relatively more dense bones which may also contribute further to demonstrate an apparent change in metabolic efficiency as body weight and FFM decrease in CED (Sims, 1986). If the range of body composition changes seen during CED influence the variable 'BMR per unit FFM', undoubtedly then the index BMR per unit FFM cannot truly reflect a change in the metabolic efficiency of the active tissues of the body. It would then appear that an increase in metabolic efficiency in the BMR component of the energy expenditure which has been hitherto considered to be the cornerstone of the beneficial, metabolic adaptation to energy inadequacy, is of doubtful existence.

Respiratory quotients (RQ) and substrate oxidation rates in chronic undernutrition

Data on RQ of chronically undernourished subjects show that individuals of poor nutritional status have a higher basal, 12 h post-absorptive, RQ compared with well-nourished controls (Shetty, 1992). The higher RQ have generally been attributed to the high-carbohydrate-containing diets consumed by them. This seems a reasonable assumption since their food quotients (FQ) also corroborate that the antecedent habitual diets of the undernourished are high in carbohydrate content. When substrate oxidation rates are calculated in these CED subjects using indirect calorimetry and urinary N excretion, it is evident that the CED subjects had significantly higher rates of carbohydrate oxidation and lower rates of fat oxidation in the fasted and fed state than well-nourished controls (Piers *et al.* 1992*b*). No differences were seen in the rates of protein oxidation; an observation that is in keeping with the evidence of similar rates of protein turnover in the CED and well-nourished subjects (Soares *et al.* 1991). Thus, CED subjects have a higher RQ largely due to their selective use of carbohydrate as fuel even in the post-absorptive, fasted state. The selective utilization of carbohydrate illustrates how closely carbohydrate oxidation is adjusted not only on its immediate availability in the diet as demonstrated in well-nourished individuals, (Flatt, 1987) but also in undernourished. This has obvious metabolic advantages to the CED individual since carbohydrate oxidation results in more ATP generation than isoenergetic amounts of fat or protein (Livesey, 1984; Elia & Livesey, 1992). Also the metabolizable energy equivalent, i.e. the energy equivalent of ATP gained (kJ/mol ATP) is almost identical to that of fat (75.3 for glycogen oxidation via glycolysis and the citric acid cycle as compared

with 79.2 for fat oxidation via β -oxidation and citric acid cycle; Elia & Livesey, 1992). Hence, it is not unlikely that the high fasting RQ of the CED reflect, to some degree, the metabolic efficiency of the active tissues of these subjects.

Analysis of several recent studies done in well-nourished and CED subjects who were weight stable was used to look at relationships between RQ and body composition variables (Shetty, 1992). Body weight, fat mass and FFM were negatively and linearly correlated with RQ. The RQ of an individual seems to reflect his body composition and particularly the available fat stores. Flatt (1972) has suggested that the anti-lipolytic effect of insulin is less effective in the presence of an increased fat mass and an increased level of insulin is, thus, associated with high free fatty acid levels in obesity. Since fat oxidation is directly related to the levels of free fatty acids (Issekutz *et al.* 1968), it is apparent that low fasting levels of free fatty acids are likely to be associated both with the small fat mass seen in CED subjects and with lower rates of fat oxidation which will contribute to the high fasting RQ. The high RQ of the CED subjects may, thus, reflect both a high dietary intake of carbohydrate, a predominant dependence on carbohydrate as fuel and a reduced rate of fat oxidation in the presence of the low fat stores.

THERMOGENESIS IN CHRONIC UNDERNUTRITION

From a conceptual point of view there are two major components of mammalian thermogenesis designated obligatory and facultative (Landsberg & Young, 1984). These two components are in turn made up of distinct sub-divisions that reflect diverse biochemical processes, fulfil different physiological roles and are regulated by several different combinations of neural and hormonal factors. Obligatory thermogenesis represents the minimal heat produced by the sum total of those processes that maintain the organism at thermoneutrality in the fasted, basal state. Facultative thermogenesis represents heat production in excess of that required to maintain the basal state, is, hence, highly variable and includes the heat produced during muscular exercise or by shivering. Facultative thermogenesis also occurs during cold exposure which is not dependent on muscular contractions or shivering, and is, hence, designated as non-shivering thermogenesis (NST). The increase in heat production that occurs after a meal is termed diet-induced thermogenesis (DIT). DIT, however, has a facultative as well as an obligatory component. The energy costs of digestion, absorption, transport and storage of the ingested meal constitute the obligatory heat production associated with the metabolic handling of the ingested nutrients. Any additional heat production that occurs following the meal is the facultative component of DIT. Both NST and the facultative component of DIT are mediated by catecholamines and regulated by the activity of the sympathetic nervous system (SNS).

NST in chronic undernutrition

Since NST is mediated via the SNS, estimation of this adaptive or regulatory component of thermogenesis is carried out by measurement of the excess O_2 consumption over the basal state when noradrenaline (NA) or adrenaline is intravenously infused. Studies on NST in CED labourers carried out by infusing three graded doses of NA showed that the undernourished had a significantly lower thermogenic response to the lowest dose, but

this effect disappeared with increasing doses (Kurpad *et al.* 1989a). Since the infusion period (30 min) was not sufficient to induce peak responses, there were no overall differences between thermogenic responses of undernourished and control subjects when compared by analysis of variance. However, infusions of a single, highest tolerable dose of NA confirmed the significantly lower thermogenic responses in the undernourished even when corrected for differences in body weight and FFM (Kurpad *et al.* 1989b). It appeared that the undernourished responded late with a steep response factor which allowed for comparable peak O₂ consumption levels to be attained. Thus, the capacity for NST remained unaltered in the undernourished (Kurpad *et al.* 1992). The preferential substrate for oxidation in the undernourished during NA infusion was carbohydrate. The suppressed thermogenesis in CED was related to the latency of the response while the ability to attain comparable peak responses in heat production was not compromised. Responses to cold exposure in CED subjects also show that their ability to increase heat production following a brief cold exposure is not compromised and that their response thresholds are also smaller than those of the well-nourished subjects. These findings are similar to the reports of reduced cold-induced thermogenesis in elderly, undernourished hospitalized patients (Fellow *et al.* 1985).

DIT in chronic undernutrition

The thermic response to a test meal depends on its energy density and nutrient composition. There are also several ways of measuring and expressing the DIT response which may alter the interpretation of the results. Hence, while measuring or expressing DIT responses for the purpose of inter-group comparisons, one is confronted with the dilemma of either administering a standard meal or a meal where energy and or protein content is based on body weight, FFM or BMR. This issue is yet to be resolved, and is further compounded by the fact that the DIT response to the same standard test meal in the same individual may show a large variability from occasion to occasion (Piers *et al.* 1992a).

Differences in facultative DIT have been invoked to explain, to some extent, the adaptive responses to alterations in energy balance in individuals. The DIT response over a 6 h period to a standard liquid meal was compared for well-nourished controls and CED subjects (Piers *et al.* 1992b). The DIT responses were highest in the undernourished subjects, both in absolute terms and when expressed as a percentage of the metabolizable energy content of the meal, i.e. when the response is corrected for the energy load administered. The non-protein RQ (NPRQ) and substrate oxidation rates were suggestive of predominant utilization of carbohydrate as fuel both in the fasted and postprandial state with little fat or protein being oxidized by the undernourished. Since CED subjects showed a lower protein oxidation rate, it is likely that the increase in DIT may in part be due to a greater increase in protein synthesis after the meal. Similar responses suggestive of an increased protein synthesis following feeding of undernourished children has been reported by Ashworth (1969). However, it has also been demonstrated that isoenergetic amounts of carbohydrate produce a higher DIT response than fat. Hence, the predominant dependence on carbohydrate as a fuel both before and after a meal may account for the higher response in the chronically undernourished. Thus, it would appear that DIT responses seen in CED are more representative of the metabolic fate of the predominant nutrient being utilized, which may in turn be

influenced by the habitual dietary intake and nutrient composition, rather than variations in facultative thermogenesis.

Recent findings on DIT measured over 15 h in Gambian subjects while in a respiration chamber, on the contrary, suggest that DIT responses are blunted in the Gambians (during the lean season) as compared with well-nourished European subjects (Minghelli *et al.* 1990). The DIT responses were neither measured using a standard meal stimulus nor were they expressed as a percentage of the metabolizable energy in the meal and may possibly be influenced by the delayed gastric emptying associated with the habitual diet of the Gambian subjects. Paradoxically, the higher RQ of these subjects indicate a greater proportion of dietary carbohydrate utilization which might be expected to induce a higher DIT response in the Gambians during the lean season. Comparisons of DIT in Gambian men in different seasons (Minghelli *et al.* 1991) have resulted in the suggestion that the DIT responses may have a possible dynamic role in modulating nutritional or seasonal influences. However, it is important to note that the subjects investigated in both these studies had mean body weights >60 kg and BMI of 20 and were unlikely to be comparable with those of the CED subjects (Piers *et al.* 1992b). In neither season (rainy or dry) did the Gambians qualify to be considered as CED by the currently accepted definition (James *et al.* 1988). These studies do not, therefore, unequivocally show that DIT response in the chronically undernourished contribute to energy saving by increasing the efficiency of energy utilization as an adaptive response.

PHYSICAL ACTIVITY IN CHRONIC UNDERNUTRITION

The physical activity component of TEE is also influenced by the nutritional status of an individual and the effects of CED on work capacity and productivity have been reviewed previously (Spurr, 1987). The contribution of the physical activity component to TEE depends on the intensity and the duration of the physical work being performed, and adaptive changes in this component may be considered under three broad categories, i.e. (1) physiological, (2) ergonomic and (3) behavioural.

Physiological adaptation

Vitteri (1971) and Vitteri & Torun (1975) compared the physical work capacity of undernourished young men with that of well-nourished army cadets and demonstrated that the former had lower V_{O_2max} and maximal aerobic power (MAP), i.e. V_{O_2max} corrected for body weight differences. However, when compared on the basis of 'cell residue' (i.e. body weight less adipose tissue, body water and bone mineral) all differences in MAP between groups disappeared. Vitteri (1971) concluded that the observed differences in MAP were the result of differences in body composition and not due to differences in cell function. Spurr (1983) summarized the results of several of his studies in Cali, Colombia which demonstrated that V_{O_2max} was lower in malnourished young adults, the degree of reduction being related to the progressive severity of malnutrition with only the severe cases of undernourished adults demonstrating a significant reduction in MAP compared with the well-nourished subjects. Spurr (1983) was also able to demonstrate that 80% of the reduction in V_{O_2max} in the moderate and severe categories of undernutrition was accounted for by differences in muscle cell mass. We have also observed a reduction in V_{O_2max} in CED subjects, which is lower than that of

the well-nourished subjects when corrected for body weight differences (R. N. Kulkarni and P. S. Shetty, unpublished results).

The reduction in maximal aerobic power of skeletal muscle cells in chronic undernutrition suggested by some of the previously mentioned studies may be the result of reduced oxidative enzyme content in skeletal muscle; a feature demonstrated in animal models of undernutrition (Tasker & Tulpule, 1964; Raju, 1974). Lopes *et al.* (1982) have shown that malnourished patients have increased muscle fatigability associated with the possibility of a decreased content of ATP and phosphocreatinine in skeletal muscle. Changes in the glycogen and total energy contents of skeletal muscle have been demonstrated in acute and chronic semi-starvation (Heymsfield *et al.* 1982). Alterations in the relative proportions of slow-twitch and fast-twitch fibres in the skeletal muscle have also been reported in undernutrition. Slow-twitch fibres have been shown to be better preserved (Lopes *et al.* 1982; Russell *et al.* 1984) while a selective reduction in fast-twitch fibres has been shown to occur in undernutrition (Henriksson, 1990). These biochemical and histological changes in skeletal muscle may account for some of the physiological changes in muscle function that have been observed in chronic undernutrition.

Assessment of endurance at 70–80% of the V_{O_2max} has also been made in malnourished individuals (Spurr, 1987). The maximum endurance time (MET) at 80% V_{O_2max} (T_{80}) was not significantly different in the three grades of malnourished subjects studied by Spurr (1987) and the T_{80} seemed to be reduced significantly following dietary repletion in the severely undernourished subjects. We have also observed no differences in MET at 85% V_{O_2max} in CED subjects compared with the well-nourished subjects (R. N. Kulkarni and P. S. Shetty, unpublished results).

Physiological responses during the recovery phase following V_{O_2max} or heavy physical activity such as endurance at 85% V_{O_2max} to exhaustion also shows several interesting features in undernutrition. CED subjects demonstrated early recovery responses after strenuous exercise (Kulkarni *et al.* 1992) and showed an absence of enhanced post-exercise rise in basal O_2 consumption the next morning, i.e. excess post-exercise O_2 consumption (Kulkarni *et al.* 1991).

Aerobic capacity is considered to be an adequate measure of an individual's work capacity and productivity. Good correlations have been demonstrated between a high V_{O_2max} and productivity in lumberjacks (Hansson, 1965), and East African and Sudanese sugar-cane cutters (Davies, 1973; Davies *et al.* 1976). Thus, productivity is affected indirectly by nutritional status through the influence of the latter on height, body fat content and V_{O_2max} . Since V_{O_2max} is related to body weight and LBM, total daily output and productivity of the CED is likely to be lower than that of the well-nourished subject. This is true even in industrial situations of less intensity than manual labour where productivity has been shown to be related to body weight and LBM (Satyanarayana *et al.* 1977).

It has been implied that part of the adaptive responses to chronic undernutrition is related to the greater efficiency at which small-sized, undernourished individuals on low energy intakes perform (Edmundson, 1980). Mechanical efficiency is the ratio between work done and the energy expended in doing it. Since it is difficult to measure work done in physiological terms, the submaximal V_{O_2} per unit body weight required to perform the task has been widely accepted as the criterion for efficiency (Cavanagh & Kram, 1985). Ashworth (1968) reported that undernourished Jamaicans had a significantly higher

gross efficiency while performing the step test. We have also reported that CED individuals have a significantly higher net mechanical efficiency than well-nourished controls while stepping (Kulkarni & Shetty, 1992). Other studies from India in undernourished subjects using the treadmill have shown that mechanical efficiency is higher in the rural undernourished as compared with urban well-nourished subjects (Satyanarayana *et al.* 1989) but have indicated that mechanical efficiency reduces as the load increases and the delta mechanical efficiency worsens in CED as the load increases (Satyanarayana *et al.* 1989; R. N. Kulkarni and P. S. Shetty, unpublished results). Spurr *et al.* (1984) have also reported increases in gross and net mechanical efficiency in smaller undernourished individuals compared with larger normally nourished controls; however, delta efficiencies of the different groups were not different. Cycloergometric assessment of physical work capacity showed that undernourished adolescents in Brazil had comparable gross mechanical efficiencies to those of the well-nourished adolescents despite poor anthropometry and an 8–15% reduced muscle mass (Desai, 1989). They were, however, able to achieve this at a higher percentage of their maximum work capacity, as evidenced by the significantly higher heart rates for the same level of O₂ consumption. The blood lactic acid levels were also higher during exercise suggesting that the available muscle mass was under greater stress to accomplish the same task which might compromise their endurance during longer time periods or higher work loads. Edmundson (1980) using the bicycle ergometer has reported that at 100 W load, the gross efficiency of Javanese on a low energy intake was significantly higher than that of men on a high energy intake. Norgan (1983) has recalculated the net mechanical efficiency from Edmundson's (1980) data and has pointed out that the group on a high energy intake had lower values for mechanical efficiency than expected and that the significant differences at 100 W output could be accounted for by the low values of the group on the high energy intake. The values obtained for delta efficiencies in the groups on the high intake in Edmundson's (1980) study are also lower than those reported for normal subjects by others (Gaesser & Brooks, 1975) and raise doubts about Edmundson's (1980) reports. Table 1 summarizes the data on mechanical efficiency in chronic undernutrition.

Ergonomic adaptation

Net mechanical and delta efficiencies of rural Gambians with mean body weights of 60.8 kg (Minghelli *et al.* 1990) are reported to be significantly higher than those of Europeans of mean body weights of 66.9 kg while walking on a treadmill at 3.2 km/h at 0 and 10% elevation. Subjective observations suggest that the vertical oscillations of the gravity centre may be reduced in Gambian men while walking. Similar ethnic differences in ergonomics may also account for the reductions of 10–17% in the cost of activities such as sitting or standing demonstrated in African and Asian subjects (Dieng *et al.* 1980; Geissler & Hamool, 1985). African women have been shown to carry loads on their heads of up to 20% of their body weight without any extra energy expenditure, which may be attributed to economic patterns of movements in these individuals (Maloiy *et al.* 1986).

Similar observations of ergonomic adaptation have been made in the low-body-weight Jamaicans studied by Ashworth (1968). When subjects were asked to move bricks, the energy expenditure involved depended on the number of bricks carried. The results of

Table 1. *Mechanical efficiency in chronic undernutrition*

		Mechanical efficiency			Work load
		Gross	Net	Delta	
Stepping					
Ashworth (1968)	Jamaica	Increased			
Kulkarni & Shetty (1992)	India		Increased		
Bicycle ergometer					
Edmundson (1980)	Java	Increased			100 W
Desai <i>et al.</i> (1984)	Brazil	No change			25-75 W
Satyanarayana <i>et al.</i> (1989)	India	Increased		Decreased	300-600 kpm/min
Treadmill					
Spurr <i>et al.</i> (1984)	Colombia	Increased	Increased	No change	3 mph; 15% gradient
Minghelli <i>et al.</i> (1990)	Gambia		Increased	Increased	3.2 kmh; 0 and 10% gradient
Kulkarni <i>et al.</i> (1992)	India		No change	Decreased	25, 50, 75, 100 W

this study showed that when the subjects were made to carry smaller loads, the energy cost increased and the cost involved was in general lowest when the subject chose his own load, i.e. the subjects, of their own choice, carried out the task that was most economical of energy use. We have made similar observations of reduced energy expenditure in CED adults, even when corrected for body weight or FFM differences, as compared with well-nourished adults (R. N. Kulkarni and P. S. Shetty, unpublished results), when CED subjects who were entrusted to complete a task such as moving bricks over a fixed distance and predetermined period of time while in a calorimeter; a task to which they were habituated. Thus, there is emerging evidence that there may be a component of ergonomic efficiency operating in the undernourished state which may be related to the pattern of locomotion, a reduction in superfluous movements contributing to an unconscious economy of activity and an element of habituation to daily tasks involving moderate to heavy physical labour. This is the component of 'real life efficiency' to which Waterlow (1986) has referred. This component of ergonomic efficiency may also explain the enhanced mechanical efficiency reported while stepping (Ashworth, 1968; Kulkarni *et al.* 1991) and while walking on a treadmill (Minghelli *et al.* 1990; Table 1). The same ergonomic efficiency may also be operating to explain the effect of a reduction in submaximal V_{O_2} , corrected for body weight differences, with age (Pate, 1981). Although small-statured individuals need to take more steps per min than taller subjects in order to maintain a given speed when stepping frequency was used as a covariate, the differences in O_2 consumption persisted, while these differences disappeared when body weight was used as a covariate. Spurr (1987) has demonstrated that in a group of normal individuals walking with or without a load, an apparent decrease in economy (i.e. increase in V_{O_2} per kg body weight) occurs with a decrease in body weight (i.e. smaller individuals appear to be uneconomical). If results of comparisons of mechanical efficiencies between well-nourished and undernourished subjects persist despite this body weight effect, then they may be attributable to changes in ergonomic efficiency which is not related to the frequency of stepping in short-statured CED subjects.

Behavioural adaptation

The behavioural adaptation that accompanies CED is mainly related to understanding how individuals allocate time and energy to different productive and leisure activities and to estimate biological and economic consequences of this change. In CED more time is given to work activities, and energy expenditure in leisure and home production activities is reduced (Immink, 1987); this is an important form of behavioural adaptation. A recent analysis of the pattern of an individual's physical activity during a voluntary reduction in food intake has shown that the behavioural response to a deficient intake was characterized by a distinct change in the activity pattern, suggesting that lower effort discretionary activities were substituted for higher effort discretionary activities while obligatory activities were not affected (Gorsky & Calloway, 1983). Torun *et al.* (1989) also arrived at similar conclusions when rural Guatemalan men with lower muscle masses were able to carry out the specific agricultural task allocated to them but took much longer to complete it. But there were other more interesting changes in their activity behaviour; these rural Guatemalans took significantly longer to walk back home after work and they spent about 3 h/d taking a nap and sitting, playing cards or doing other sedentary activities. In contrast, the better-nourished age-matched males did not nap, were active at home and played soccer and remained physically active for a significantly greater proportion of the day. Marginally-undernourished individuals tend to become more sedentary and spend less time on social interactions and discretionary non-salaried activities. Latham (1989), in a summary of his observations of 220 male road workers in Kenya, also stated that nutritional status was related to the time taken to complete a task. Men with low weight-for-height values took longer to complete the same task than men with a higher weight-for-height. Latham (1989) concluded that energy-deficient individuals will be forced over a period of time to limit their activities. They forego activities to conserve energy, some of which they do consciously and wilfully, some they do unconsciously.

More recent findings based on two concurrent studies (Branca *et al.* 1992; Norgan *et al.* 1992) of seasonal variations in the activity patterns of adults (men and women) in rural India and Ethiopia showed that a large percentage of individuals with varying grades of CED spent less time per day working as compared with individuals in the same socio-cultural milieu who were better nourished and support the impression that behavioural adaptation of spontaneous, free-living physical activity in fact occurs in CED subjects. Restricting physical activity is an important strategy for low-weight individuals but rather than being beneficial it may jeopardize their survival under stress conditions when sudden demands are placed on them.

Reversibility of adaptive changes in chronic undernutrition following supplementation

Studies on experimental semi-starvation have shown that increase in BMR is associated with refeeding of semi-starved individuals (Grande, 1964). It has been observed that much of the increase occurs, in both the activity and quantity of visceral tissues such as liver, which are the earliest to show increases during refeeding. Supplementation of CED subjects over a 12-week period has shown that nearly 70% of the increase in body weight seen over the total period of 12 weeks, occurred during the first 3 weeks (Soares *et al.* 1992). The increase in BMR was larger than that accounted for by the increase in FFM. It was apparent that an increase in muscle mass did not contribute much to the observed

Table 2. *Effects of supplement on physical activity in adult chronic undernutrition*

Country	Study	Physiological variable	Finding	References
Guatemala	S v. UnS	V_{\max} , MAP	No change	Vitteri (1971)
Colombia	pre-S v. post-S	V_{\max} , MAP, MET (T_{80})	Improved Reduced	Barac-Nieto <i>et al.</i> (1980) Spurr (1983)
Brazil	pre-S v. post-S	PWC	Improved	Angeleli <i>et al.</i> (1983)
India	pre-S v. post-S	V_{\max} , MAP, MET (T_{85})	Unchanged	Kulkarni & Shetty*

S, supplemented; UnS, unsupplemented; pre-S, presupplementation; post-S, post-supplementation; MAP, maximal aerobic power; MET, maximum endurance time (T_{80}/T_{85} signify at 80% or 85% V_{\max} ; PWC, physical work capacity.

* Unpublished results.

increases in FFM. RQ >1.0 were seen during the early period suggesting enhanced lipogenesis which coincided with the rapid increase in fat mass. RQ dropped to near presupplementation levels around the period when the fat mass stabilized (i.e. 6–9 weeks) despite continuation of the supplement for a further period of several weeks. Estimation of substrate oxidation rates demonstrated enhanced carbohydrate oxidation and net lipogenesis in the post-absorptive, fasted state (Piers *et al.* 1992c).

The thermogenic response to NA was unaltered in the CED subjects after 12 weeks of supplementation (Vaz *et al.* 1990); DIT responses to an identical meal stimulus also showed no differences at the end of the supplementation period (Piers *et al.* 1992c). Studies in The Gambia, however, seem to suggest that some blunting of DIT responses occurs in the Gambians during the lean season (Minghelli *et al.* 1990).

Several studies have investigated the effects of supplementation on physical activity, work performance and productivity. Spurr (1983) demonstrated an increase in $V_{O_2\max}$ following dietary repletion along with an associated reduction in maximum endurance time. We have observed no change in either $V_{O_2\max}$ or endurance time following 12 weeks of supplementation (R. N. Kulkarni and P. S. Shetty, unpublished results). Angeleli *et al.* (1983) have observed an increase in physical work capacity with supplementation. Table 2 summarizes some of the findings for the physiological variables of physical activity following supplementation. Studies of German (Kraut & Muller, 1946) and Kenyan (Wolgemuth *et al.* 1982) labourers have shown that supplementation of their diets elicited increases in productivity. Immink *et al.* (1981) were unable to demonstrate differences in productivity between supplemented and unsupplemented groups. Diaz *et al.* (1991) using a cross-over design were also unable to show any significant impact on the productivity variables with supplementation. Critical evaluation of the effects of supplementation on work output and productivity is not possible here since many of the studies are so different, the variables changed from study to study and none appeared to be sufficiently robust in design or execution to settle this issue once and for all.

CONCLUSIONS

BMR of chronically undernourished individuals are lower than those of the well-nourished subjects but not different when corrected for differences in body weight or FFM. BMR per kg FFM, hitherto considered the definitive index of metabolic efficiency, is not altered during chronic undernutrition and there is, thus, no evidence of an

enhanced metabolic efficiency in the undernourished. The index does not truly reflect changes in the efficiency of energy utilization of the active tissues of the CED, but is perhaps an artefact resulting from the changes in the composition of the body, particularly a disproportionate alteration in muscle mass. Hence, it is unlikely that the existence of an enhanced metabolic efficiency is demonstrable in the chronically energy-deficient state. However, elevated post-absorptive, fasted RQ of the undernourished indicate a predominant dependence on carbohydrate utilization even in the fasted state, which may enhance to some degree the efficiency in energy utilization at the tissue or organ level. This may be related to high levels of carbohydrate in their habitual diets as well as to low fat stores. The capacity for NST is not compromised in the CED, although they show response characteristics which are different from those of the well-nourished individuals. DIT responses to the same meal stimulus seem to be enhanced, possibly by greater postprandial protein synthesis. V_{O_2max} is lower in undernourished subjects, proportionate to the reduction in muscle mass of individuals. New findings suggest that in the chronically undernourished there are subtle changes in O_2 debt and recovery responses after exercise, as well as an absence of excess post-exercise O_2 consumption. Ergonomic or real-life efficiency and behavioural alterations may also contribute to energy sparing. Energy supplementation has varied effects on the three components of TEE; BMR increases without any significant change in the thermogenic component. The responses in physical activity and their contributions to productivity seem to vary among the several supplementation studies evaluated. Metabolic adaptation, in the sense of enhanced metabolic efficiency, is not readily demonstrable in the chronically undernourished state. Thus, there is a need to reappraise our concepts of metabolic adaptation in chronic energy deficiency and the models suggested by Ferro-Luzzi (1985) are no longer appropriate and may need to be revised.

The inability to demonstrate meaningful, adaptive responses in the three components of energy expenditure, BMR, thermogenesis and physical activity in chronically undernourished subjects is not surprising since none of them may be of significant benefit to the individual in terms of enhanced metabolic or physiological efficiency. The lack of any convincing demonstration of enhanced metabolic efficiency in BMR would imply that contribution to the other two components is limited. Thermogenesis shows equivocal responses while physical activity component is considerably compromised, thus affecting productivity and wage-earning abilities. There is no rigorous evidence of increased mechanical efficiency of muscular work or its improvement with supplementation; there may, however, be some savings from real-life efficiencies and from behavioural alterations which may contribute to an economic pattern of work or life-style which may impart some degree of energy saving.

The evidence reviewed here would support the existence of adaptive changes in body size and body composition, i.e. short stature, low body weight, low BMI, low fat stores, and possible changes in spontaneous physical activity by behavioural or life-style responses as being important changes that occur during the evolution of the chronically energy-deficient state. Neither of these two adaptive responses confer any great functional benefit to the individual except to further his survival under marginal or sustenance conditions. These are not acceptable as beneficial adaptations which justify the continuation of the energy-deficient state. As Waterlow (1986) stated, 'it is almost impossible to discuss adaptation without making value judgements and without using indefinable concepts such as "normal", "healthy", "satisfactory", etc. D'Arcy

Thompson said, "sooner or later nature does everything that is physically possible. Our problem is, that which is physically possible may not be good enough".'

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