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Review

Adipose tissue heterogeneity: Implication of depot differences in adipose tissue for obesity complications

Mi-Jeong Lee, Yuanyuan Wu, Susan K. Fried *

Section of Endocrinology, Diabetes, and Nutrition, Department of Medicine, Boston University, School of Medicine, Boston, MA 02118, United States

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ABSTRACT

Obesity, defined as excess fat mass, increases risks for multiple metabolic diseases, such as type 2 diabetes, cardiovascular disease and several types of cancer. Over and above fat mass *per se*, the pattern of fat distribution, android or truncal as compared to gynoid or peripheral, has a profound influence on systemic metabolism and hence risk for metabolic diseases. Increases in upper body adipose tissue (visceral and abdominal subcutaneous) confer an independent risk, while the quantity of gluteofemoral adipose tissue is protective. Variations in the capacity of different depots to store and release fatty acids and to produce adipokines are important determinants of fat distribution and its metabolic consequences. Depot differences in cellular composition and physiology, including innervation and blood flow, likely influence their phenotypic properties. A number of lines of evidence also support the idea that adipocytes from different anatomical depots are intrinsically different as a result of genetic or developmental events. In this chapter, we will review the phenotypic characteristics of different adipose depots and mechanisms that link their depot-specific biology to metabolic complications in men and women.

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Abbreviations: VAT, visceral adipose tissue; SAT, subcutaneous adipose tissue; sc, subcutaneous; SVC, stromal vascular cells; CLS, crown like structures; LPL, lipoprotein lipase; GLUT4, glucose transporter 4; VLDL, very low density lipoprotein; TG, triacylglyeride; FFA, free fatty acids; TNF-α, tumor necrosis factor-alpha; IL-6, interleukin-6; SAA, serum amyloid A; RBP4, retinol binding protein 4; MCP-1, macrophage chemoattractant protein-1; CRP, C-reactive protein; GM-CSF, granulocyte-macrophage colony stimulating factor; TSP-1, thrombospondin 1.

* Corresponding author. Address: Division of Endocrinology, Diabetes, and Nutrition, Department of Medicine, Boston University, School of Medicine, 650 Albany St., EBRC-810, Boston, MA 02118, United States. Tel.: +1 617 638 7110; fax: +1 617 638 7124.

E-mail address: skfried@bu.edu (S.K. Fried).

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1. Adipose tissue anatomy and distribution

1.1. Adipose tissues are present in discrete depots throughout the body

The adipose organ includes numerous discrete anatomical depots (Shen et al., 2003) (Fig. 1). The size of fat stores is highly variable, ranging from 5% to 60% of total body weight. Subcutaneous adipose tissues (SAT) store >80% of total body fat in the body. The most commonly defined and studied subcutaneous (sc) depots are the abdominal, gluteal and femoral. A layer of connective tissue (Scarpa's fascia), visible on computerized tomography (CT) separates deep from superficial sc fat. These sc layers are functionally distinct and independently correlate with metabolic complications of obesity (Smith et al., 2001).

Intraabdominal fat depots are associated with internal organs. In humans, intra- and retro-peritoneal depots represent 10–20% of total body fat in men and 5–10% in women. Intraperitoneal or so-called visceral adipose tissues (VAT) are associated with digestive organs, and include the omental (hangs off the stomach), the mesenteric (associated with the intestine), and epiploic (along the colon).

There are also numerous smaller adipose depots such as epicardial and intermuscular that may serve specialized functions related to their neighboring tissues (Sacks and Fain, 2007; Cinti, 2001). Recent literature (re)discovered the presence of brown adipose tissues (BAT) in adult humans. BAT is found in cervical-supraclavicular, perirenal, and paravertebral regions. Unlike white adipocytes which have mesenchymal or pericyte origins (Tang et al., 2008), brown adipocytes are derived either from myogenic lineage or trans-differentiation from white adipocytes ("brite") (Kajimura et al., 2010). While BAT plays critical role in cold-induced thermogenesis, its potential in the control of adaptive thermogenesis, body weight and metabolic disorders in humans has not been yet proven (Ravussin and Galgani, 2011).

1.2. Cellular composition of adipose tissues

White adipocytes are characterized by a unique morphology with unilocular lipid droplets that occupy 95% of the cell volume and thereby determine the cell size, which ranges from ~20 to 200 μm. Other cell types are also present within ATs. These stromal vascular cells (SVC), usually isolated after collagenase digestion, include preadipocytes, endothelial cells, pericytes, as well as various immune cells (macrophages, T-cells, neutrophils, lymphocytes). Multipotent stem cells are also present and due to easy access, the potential of AT in regenerative medicine has been proposed. Although other cells outnumber adipocytes in the tissue (1–2 million adipocytes and 4–6 million other cells are present in a gram of human AT), adipocytes constitute ~90% of the tissue volume. VAT includes an abundance of milky spots and lymph nodes where lymphocytes accumulate (Gabrielsson et al., 2003; Litbarg et al., 2007). Thus, Pond hypothesized that VAT plays a special role in immunity, potentially explaining the growth of VAT in response to infections such as HIV (Pond, 2005). Visceral as well as epicardial AT also include mesothelial cells (Darimont et al., 2007; Sacks and Fain, 2007). Undoubtedly, depot-differences in cell populations contribute to depot-differences in adipokine production, and can contribute to variations in adipocyte function via paracrine interactions.

2. Determinants of fatness and fat distribution

Race, sex and age affect AT distribution. However, the mechanisms involved are barely understood.

2.1. Sex differences

Women generally have higher adiposity than men. In addition, men accumulate more fat in central area (both VAT and abdominal sc), while women accumulate more in lower body sc (gluteofemoral) (Geer and Shen, 2009). Factors that govern

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