

Connecting nutrient sensing and the endocrine control of metabolic allocation in insects

Erik C Johnson, Jason T Braco and Matthew A Whitmill

It is clear that specific hormones control an organism's energy use and regulate the differential allocations of energy to activity, growth and maintenance of specific tissues, and reproduction. Appropriate metabolic allocations require an assessment of the nutrient state of the animal, and nutrient sensing must be tied to appropriate signals in order to coordinate the repertoire of behaviors and physiologies accompanying a particular metabolic investment. Here, we review the known and speculated connections between nutrient sensing and the endocrine control of energy allocation in insects. Insects, being speciose and diverse in life history strategies, offer a unique perspective into the general architecture of the signaling mechanisms of energetic allocation and also into unique elements that correlate with specific life histories.

Addresses

Department of Biology, Wake Forest University, Winston-Salem, NC 27109, USA

Corresponding author: Johnson, Erik C (johnsoec@wfu.edu)

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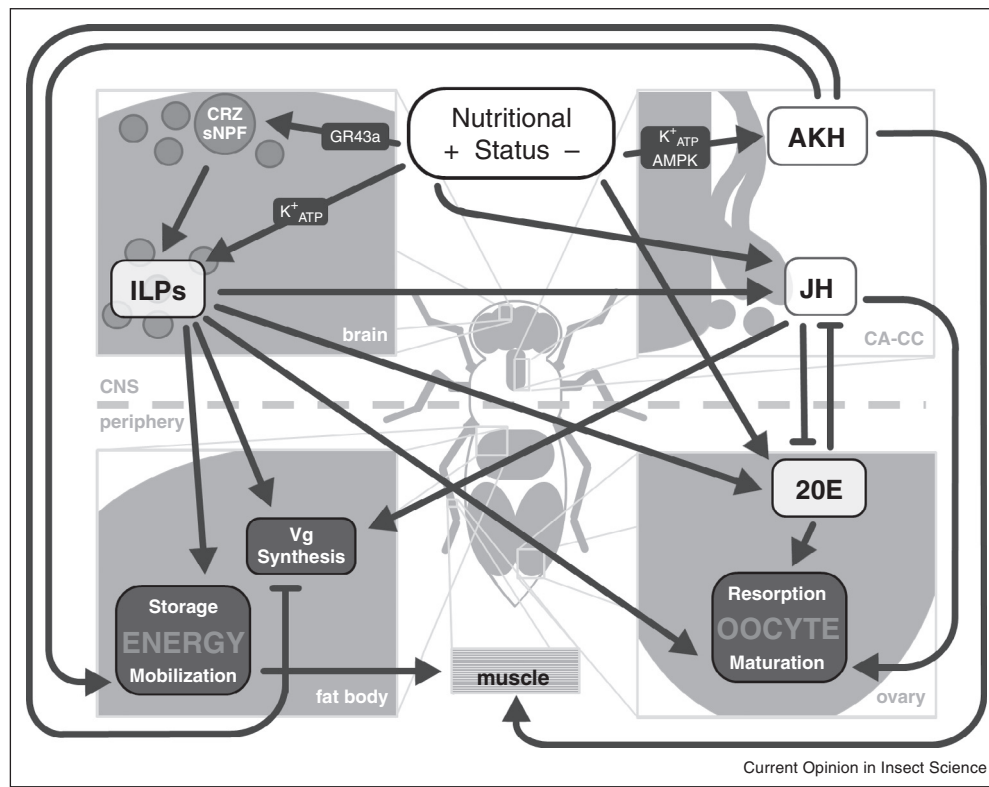
The decision of how to allocate energy is an inescapable reality for all organisms. In the broadest sense, there are limited biological uses for energy: it can either be stored for later use, or be mobilized either for growth and maintenance, reproduction, or flight. Heightened locomotor activity is energetically demanding, yet occurs routinely in the insects, and can be extreme as occurs following exposure to inhospitable environs or during the remarkable migrations by members of Lepidoptera and Orthoptera. Growth in the insects is also diverse, from the ametabolous insects to the complete metamorphosis in holometabolous orders. Growth during development requires energy investments, as does the maintenance of adult tissues. Reproduction is also energetically expensive and represents a pivotal life-history 'trade-off' in metabolic investment.

Insects are incredibly diverse, and within this class, multiple reproductive and life history strategies have evolved. Therefore it follows that studies in various insect models have the promise to provide insight into both the conserved and the unique mechanisms for understanding metabolic pathway in the context of life history strategies. Despite the incredible diversity of insects, it is apparent that there are general themes that emerge regarding the mechanisms of how energy is allocated toward different physiologies and behaviors. The specific endocrine and signaling mechanisms have been highly conserved, and thus offer insight into the general architecture of metabolic allocation pathways. Likewise, the diversity within insect orders also offers insight into the elements that correlate with different life history structures, from eusociality, migratory behaviors, to the rich diversity of reproductive differences exhibited in the insects from classical 'R' to 'K' models [1,2].

With the advent of multicellularity, metabolic decisions required precise coordination between different systems, and endocrine factors are well suited to effect the communication between functionally specialized systems. While it is tempting to label such endocrine factors generically (e.g. 'insulin is a growth hormone') this typically fails to recognize the full functional scope of each particular hormone. Indeed, as an example, the corticotropin releasing factor hormone was isolated in insects based on its effects on diuresis [3], however to call it diuretic hormone, DH, is to neglect an expanding functional repertoire of this endocrine factor. In addition to hormone pleiotropy, a single hormone is unlikely to be the sole arbiter of entire metabolic decisions; it is instead much more likely that this decision is mediated by a signaling network, which allows the inputs of multiple factors to facilitate a 'metabolic' decision.

Metabolic decisions require the sensing of the nutritional state of the organism. Here, we discuss endocrine factors that are likely critical for the integration of multiple sensory inputs that relay nutritional status and coordinate these important metabolic decisions. This is not a comprehensive review of these hormones and their modes of action but rather a brief commentary on the specific endocrine factors that either directly possess nutrient sensing mechanisms or do so indirectly through other factors. In turn, these endocrine factors coordinate downstream tissues (including the fat body and female ovary) to regulate their actions in a metabolically dependent fashion (Figure 1).

Figure 1



Neuroendocrine pathways directing differential energy allocation in response to nutritional status. JH and ILP levels are increased in response to positive nutritional status, whereas 20E and AKH are increased in response to negative nutritional status. Relevant cell autonomous nutrient sensors are indicated by arrows. In the fat body, these hormones control the rate of vitellogenin synthesis (JH, ILP's) and direct fatty acid anabolism (ILP's) and catabolism (AKH). In the ovary, these hormones direct oocytes through a critical developmental window where they must either continue maturation (JH) or be resorbed (20E).

Adipokinetic Hormone

Adipokinetic Hormone (AKH) figures prominently in the mobilization of energy from the fat body. This peptide hormone is found throughout the Arthropods, and in insects is specifically produced in the cellular component of the corpus cardiacum, an endocrine gland [4–6]. There are different numbers of AKH peptides in different insect species, ranging from three in the locust, to a single member in *Drosophila* [7]. In the honeybee, there is a disruption of the promoter element in the AKH gene, leading to non-detectable levels of this hormone [8]. While this may be a product of the unique eusocial structure of this Genus, it may, in addition, reflect the unique aspects of foraging strategies and behaviors exhibited by this insect. More detailed discussions of AKH in the insect can be found in the following references [4–6].

The neuroendocrine cells that express AKH are critical for integrating internal and external signals of metabolic state. Specifically, in *Drosophila*, these cells are intrinsically sensitive to sugars [9,10] and are activated under low sugar conditions, which leads to elevated hormonal release, thereby liberating 'energy' from stored reserves

through the hydrolysis of glycogen and fatty acids. Exactly how AKH cells 'sense' low hemolymph trehalose is unclear, although in *Drosophila* the AMP-activated protein kinase functions in potentiating AKH release when energy levels are low [10]. Furthermore, involvement of an ATP dependent K^+_{ATP} channel has also been implicated as a critical sensor for internal metabolic status in these cells in *Drosophila* [9]. These results suggest the existence of two independent internal indicators of nutrient status in this cell type, and future studies should test this hypothesis in other insects. Likewise, many endocrine factors have been shown to facilitate AKH secretion, including the peptides, CCAP, proctolin, tachykinin, and octopamine [11–14] and thus these and other hormones may relay nutrient status.

AKH, being a small peptide hormone, binds to a G protein coupled receptor, which shares significant sequence similarity with the vertebrate Gonadotropin releasing hormone receptor family [15]. The receptor is highly expressed in the insect fat body, where binding of AKH activates calcium (via the Phospholipase C pathway) and cyclic AMP signaling pathways, leading to the

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