

Molecular mechanisms of phenotypic plasticity in social insects

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Polyphenism in insects, whereby a single genome expresses different phenotypes in response to environmental cues, is a fascinating biological phenomenon. Social insects are especially intriguing examples of phenotypic plasticity because division of labor results in the development of extreme morphological phenotypes, such as the queen and worker castes. Although sociality evolved independently in ants, bees, wasps and termites, similar genetic pathways regulate phenotypic plasticity in these different groups of social insects. The insulin/insulin-like growth signaling (IIS) plays a key role in this process. Recent research reveals that IIS interacts with other pathways including target of rapamycin (TOR), epidermal growth factor receptor (Egfr), juvenile hormone (JH) and vitellogenin (Vg) to regulate caste differentiation.

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Introduction

Polyphenism in insects, in which a single set of genes is capable of producing more than one distinct phenotype in response to environmental cues, is a captivating phenomenon that did not fit easily into reigning biological paradigms during the dominance of population genetics in the last century [1]. Social insects are especially intriguing examples of polyphenisms because their responses to social cues enable them to integrate their societies to the point that selection acts above the individual at the level of the colony [2]. The best studied of these is the European honey bee (*Apis mellifera*). The combination of a new generation of sequencing techniques and powerful bioinformatic tools has allowed rapid advances in the

understanding of not only the genes involved in determining alternative phenotypes but also the processes that regulate gene expression.

Major factors involved in phenotypic plasticity in social insects

Phenotypic plasticity associated with reproductive division of labor is a key feature of eusociality [3,4]. Different lineages of social insects have evolved eusociality independently [4] raising the question of whether the mechanisms underlying the development of polyphenic castes are conserved among these groups. Comparative expression analyses of major lineages of social insects have revealed that conserved pathways are associated with the development of alternative castes [5]. Such pathways include interactions among the insulin/insulin-like growth signaling (IIS), target of rapamycin (TOR), major insect hormones (juvenile hormone (JH) and ecdysteroids), storage proteins (e.g. vitellogenin (Vg) and hexamerins) and metabolic pathways [5–10,11[•],12,13,14^{••},15].

Although similar pathways control caste polyphenism, there are important differences in their regulation among different lineages. External stimuli such as nutrition and temperature have different influences on caste determination. The effect of nutrition is predominant during caste determination in most groups of bees [7,16,17], wasps [18[•]], termites [19] and ants [20]. In *Polistes* wasps, the mechanisms regulating diapause and reproductive division of labor are closely associated, that is, nourishment along with social behavior determine caste [18[•],21,22]. Dominance behaviors may exert their biasing effects through nutrition. For example, dominant females make vibratory movements during larval feeding [22] that may act as a stressor, which by inhibiting nutrition results in the development of worker phenotypes [23,24]. On the other hand, temperature has been shown to influence caste determination in some ants of temperate climates [11[•],25]. The potential effect of temperature on caste determination remains to be determined in other groups of social insects, although there is evidence of temperature-associated seasonal effects on IIS, TOR, JH and Vg that result in different physiological and behavioral phenotypes in adult worker honey bees [26–28].

Another difference among groups of social insects is the impact of the genetic background. Genotypic differences among individuals influence caste determination in different groups of ants and bees [29,30]. For example, while strict genetic caste determination occurs in some hybrid

populations of the harvester ants *Pogonomyrmex barbatus* and *P. rugosus*, both genetic and environmental factors influence caste determination in other populations of these two species and in other ants of the genus. In *P. badius*, genetic factors influence both caste and size, but larval nutrition is better in reproductive females compared with workers, and in major compared with minor workers. Similarly, in *P. rugosus*, genetic compatibility [25], temperature and nutrition affect caste determination [11**]. In this species, hibernation increases expression of Vg and ILP genes, and treatment with methoprene (JH analog) mimics hibernation [11**].

These results suggest that in species where both genetic and environmental factors influence caste determination, this process is still mediated by similar pathways than species where caste determination is exclusively or predominantly controlled by nutrition (e.g. honey bees). For example, in the bee *Melipona quadrifasciata*, which has genetic determination, JH has been shown to have a critical role in caste determination [31]. The involvement of JH suggests interactions with the IIS pathway as is known to occur in other social insects [11**,32].

In addition, social insects show differences in pathway regulation that include alternative utilization of proteins of similar function or differential duplication and subfunctionalization of such proteins. For example, in honey bees differential larval nutrition associated with caste determination is influenced by the consumption of proteins secreted by the hypopharyngeal gland, especially major royal jelly protein 1 (MRJP1, the predominant protein of royal jelly) [33,34]. In ants, where workers do not produce royal jelly, maternally inherited Vg influences caste determination, presumably by playing a similar nutritional role [11**]. In highly eusocial ants and termites, Vg experienced gene duplication and subfunctionalization to acquire specific functions associated with different caste and behavioral phenotypes [14,35,36]. However, it remains to be determined whether Vg can play the role of MRJP1 as activator of the epidermal growth factor receptor (Egfr) pathway [33] and subsequent downstream JH signaling during caste determination in these groups of social insects (Figure 1).

Insulin signaling pathway – from nutrition through caste differentiation

Nutritional state of insects is reflected in responses of the IIS pathway. TOR and Egfr pathways join or network with the IIS pathway: the TOR pathway senses amino acids, and Egfr signaling plays roles in growth and development (Figure 2). IIS, TOR and Egfr systems have been shown to play roles in caste determination in bees [33,37], as well as in control of size in worker ants [38]. RNAi knockdown of IRS, TOR and Egfr in queen-destined larvae results in the expression of more worker-like characters, demonstrating their importance [33,37–40].

Individual elements of the IIS pathway are important in modulating its signals. Beginning at the head of the IIS pathway, honey bees and fire ants each have two insulin-like proteins (ILPs) and two insulin receptors (InRs) [7,41–44]. The ILPs in bees are regulated independently: ILP1 knockdown decreases JH levels, and ILP2 knockdown reduces ovary size [45]. In fire ants, the two InRs differ in expression between castes during development and in sequences governing post-translational modifications [42].

Differences in expression between queen and worker larvae early in development indicate key factors initiating caste determination. ILP1, InR2, tuberous sclerosis 1 (TSC1), and TOR are more highly expressed in queen larvae at 40 hours post-hatching [7,46]. The importance of InR2 and TOR activity is also demonstrated by the decrease of JH levels after knockdown of these proteins [37,39]. Cameron *et al.* (2015) [47] extended information about expression back until six hours after newly hatched larvae were grafted into queen cells. At that point substantial differences in gene expression were detected between queen and worker larvae. Early in development, larvae become biased toward one caste or the other but do not commit until later in development; thus early caste-specific development is reversible. The finding of two distinct development phases is consistent with earlier molecular studies [48,49].

Future research will undoubtedly reveal additional pathways that connect IIS, TOR and Egfr to growth and differentiation. One candidate in honey bees is the hypoxia network, which regulates oxidative metabolism. Its elements are differentially expressed in worker and queen larvae [50]. Also, the highly conserved Fat/Hippo signaling pathway appears to link IIS to growth of polyphenic horns in rhinoceros beetles and mandibles in stag beetles [51].

Epigenetics and caste

The IIS pathway and juvenile hormone are central to caste determination, but their differential effects may not be maintained without further downstream processes. In the past decade, epigenetic modifications of DNA as mechanisms for controlling phenotype have been investigated. If the DNA methylation system is compromised by knocking down one of its key enzymes, Dnmt3, nutrition that normally evokes the worker developmental program, fails to do so and queens or queen-like adults result [52]. This suggests a role for DNA methylation in caste differentiation, which has been supported by findings of caste-specific methylation in adults and larvae of several species of ants and bees [53–56]. However, such reports come exclusively from studies lacking biological replication. Furthermore, the only replicated studies of differential methylation (performed in adults) did not detect differences between queen and worker brains

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