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Epigenetic in Insects

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A B S T R A C T

Epigenetic in insects is an important origin of biodiversity that can convert environmental stimuli into heritable phenotypic changes and biological variation without mutations and independent changes in the DNA sequence, by variation of gene expression levels. Epigenetic may play important roles in the parameters such as development, longevity, reproduction, gender-specific phenotypic variation, immunity, and evolution of both insect-plant and insect-microbe interactions. To investigate the molecular bases of epigenetic, social insects like ants provide a natural experimental system. In social insects, multiple phenotypes and distinct types of individuals arise from a single genome. The existence of alternative phenotypes encoded by the same genome is known as polyphenism. Caste polyphenism is originated from molecular information that once established can be later maintained through epigenetic inheritance. As well as, Host–parasite interactions are intimate epigenetic relationships. Insect Epigenetic mechanisms are divided in to before transcription and post-transcriptional gene regulation. DNA methylation and histone acetylation/deacetylation are before transcription and small non-coding RNAs known as microRNAs are referred to as post-transcriptional gene regulation. Methylation is common throughout the genome and it is reported as the origin of differential gene expression in social insect castes. In general, insects possess relatively low levels of DNA methylation, compared to mammalian systems. Epigenetic studies in insects are not only progressing but also promising to find a solution for pesticide resistance.

Introduction

Epigenetic has been recognized as changes in tissue-specific gene expression (but not gene sequence) in eukaryotes due to different environmental stressors. It can lead to heritable phenotypic changes across generations and adaptation in natural populations (Gadjev, 2015; Vilcinskas, 2016).

Epigenetic regulation converts environmental stimuli into heritable phenotypic changes and biological variation without mutations and independent changes in the DNA sequence, by variation of gene expression levels. Epigenetic may play important roles in the parameters such as development, longevity, reproduction, gender-specific phenotypic variation, immunity and evolution of both insect-plant and insect-microbe interactions (Lemos et al., 2010; Mukherjee et al., 2015; Bingsohn et al., 2016; Kim et al., 2016; Peleg et al., 2016; Reynolds et al., 2016). Epigenetic information cause insect host-parasite coevolution, however, it is unclear how exactly offspring could receive this information from the parents (Cheeseman and Weitzman, 2015; Pigeault et al., 2016; Vilcinskas, 2016).

Interestingly, after the establishment of a feature, transcriptional patterns that define cell identities could be stable over long periods of time even if the originating stimuli such as environmental cues, developmental signals, infection, etc. have disappeared. The chemical changes on chromatin and the manner that patterns of gene expression remain are the central research topic of the epigenetics. Indeed, epigenetics studies the inheritance of phenotypic traits that do not require changes in the primary DNA sequence (Bonasio and Reinberg, 2010).

Epigenetic phenomena in insects have long been studied decades before most biologists had ever even heard of “epigenetics” (Burggren, 2017). In insects,

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abiotic stressors including starvation, mild heat shock, and toxins, as well as biotic stressors such as infections, could affect gene expression changes in genes encoding stress or immunity-related proteins (Freitak et al., 2012; Vandegehuchte and Janssen, 2014).

While epigenetic could influence cell development, cell cycle regulation, cell state, and cell fate, there are increasing interest in research on epigenetic regulation at the molecular, cellular, tissue and organ levels in insects (Chen et al., 2017). To investigate the molecular bases of epigenetic, social insects like ants provide a natural experimental system.

In social insects, multiple phenotypes and distinct types of individuals arise from a single genome. Castes are alternative phenotypic classes with different morphology, reproductive physiology, and biology, behavior and lifespan (10-fold longer for queens compared with workers) (Keller and Genoud, 1997). This phenotypic diversity and flexibility were identified by a single genome. Female embryos become either reproductive queens or various types of workers, and interestingly it does not depend on their genome. The existence of alternative phenotypes encoded by the same genome is known as polyphenism. Caste polyphenism is originated from molecular information that once established can be later maintained through epigenetic inheritance (Bonasio, 2014).

Ant queens and males that are assumed as reproductive casts have wings, but sterile workers are wingless (Ho¨lldobler and Wilson, 1990). Reproductive casts have a conserved and active transcriptional network that specifies wings. This transcriptional network is interrupted in sterile workers without underlying genetic differences. All individuals have the genetic information for the polyphenic traits, but some signals could activate them and maintenance of them will be due to epigenetic, means even when there is not appropriate signal anymore (Weiner and Toth, 2012).

The goal of this review was to introduce epigenetic and its inheritance systems (including chromatin modifications, DNA methylation, and MicroRNAs) in insects. As well as, epigenetic interaction between “insects and their symbionts” and “insects and their parasites” were reviewed.

DNA methylation

Epigenetic mechanisms are divided in to before transcription and post-transcriptional gene regulation. DNA methylation and histone acetylation/deacetylation are before transcription and small non-coding RNAs known as microRNAs (miRNAs) are referred to as post-transcriptional gene regulation (Jaenisch and Bird, 2003; Gomez-Diaz et al., 2012).

DNA methylation is an epigenetic mechanism that works before the transcription begins. The addition of a methyl group to a cytosine residue in the dinucleotide sequence CpG forms 5-methylcytosine, which the base-pairing capacity of the unmodified nucleoside preserves but interaction with regulatory proteins will change. Transcription of the downstream genes could be inhibited and gene silencing occurs significantly by methylation of even a single CpG site in a promoter region (Robertson et al., 1995).

DNA methylation is widespread and generally occurs across all domains of life such as vertebrates and flowering plants, many prokaryotes and some fungi and protozoa. In different invertebrates, such as Arthropoda (He et al., 2015) and Mollusca (Gavery and Roberts, 2010) cytosine methylation plays an important role in epigenetic by gene regulation (Goll and Bestor, 2005).

DNA methylation has been revealed in different insect orders such as Coleoptera, Diptera, Lepidoptera, Hemiptera, Hymenoptera, Orthoptera and Odonata (Xiang et al., 2010; Zhang J. et al., 2015; Zhang M. et al., 2015). Methylation is common throughout the genome and it is reported as the origin of differential gene expression in social insect castes (Elango et al., 2009; Foret et al., 2012).

DNA methyltransferases (DMNTs) are enzymes that add a methyl group to individual nucleotide bases of DNA in chromosomes. DNMT1, DNMT2, and DNMT3 are three families of these enzymes. DNMT1 and DNMT2 are widespread among different insects, due to being evolutionarily conserved, whereas only some hymenopteran and hemipteran species have DNMT3 (Glastad et al., 2011). Some insects including mosquitoes such as Drosophila melanogaster (Ye et al., 2013), Anopheles gambiae (Holt et al., 2002) and Aedes aegypti (Nene et al., 2007) have only DNMT2, however all three DMNTs are reported from honey bee genome plus a duplicated copy of DNMT3 (Lyko and Maleszka, 2011).

Genome-wide methylation analysis in some insects such as the parasitic wasp Nasonia vitripennis, the silkworm Bombyx mori and the honeybee Apis mellifera, has revealed that 5-methylcytosine is the most common DNA variation (Cingolani et al., 2013; Xiang et al., 2013; Beeler et al., 2014). The highest degree of CpG methylation was happened in the embryos of A. mellifera and Tribolium castaneum and was reduced gradually in the other developmental stages (Drewell et al., 2014; Feliciello et al., 2013).

Using bisulphite sequencing can identify specific methylated genes. Genome-wide studies have shown that in insects the ratio of methylated to unmethylated CpG is much lower than vertebrates (Lyko et al., 2000). In the fruit fly Drosophila

melanogaster less than 0.5% of cytosine residues in the CpG dinucleotide are methylated (Marhold et al., 2004). In general, invertebrates possess relatively low levels of CpG sites methylation (0.36–20%) (Regev et al., 1998), compared to mammalian systems (60–90%) (Suzuki and Bird, 2008).

Different studies have shown that DNA methylation is often restricted to genic regions (promoters, exons, and introns) of the genome and not intergenic regions (Suzuki and Bird, 2008). In invertebrate genomes, such as hymenopteran insects (ants, bees and parasitoid wasps), low levels of DNA methylation occur within transposable elements (TEs), compared to vertebrate genomes (Yan et al., 2015). Methylation in the aphids, A. aegypti, and honey bee genome occurs in the promoters of genes, therefore it could reduce transcription and metabolism (Ye et al., 2013).

Several studies have proposed that in insects, alternative splicing of gene and also gene activation associated with DNA methylation. For instance, alternative splicing of mRNA transcripts due to DNA methylation could lead to behavioral regulation and caste specificity in eusocial insects including termites (Terrapon et al., 2014), bees (Foret et al., 2012; Li-Byarlay et al., 2013) and ants (Bonasio et al., 2012). As well as, loss of DNA methylation from esterase gene of the green peach aphid Myzus persicae led to the reduction of transcription of this insecticide-detoxifying.

Chromatin modifications

There are some proteins in the eukaryotic cell nuclei known as Histones that compose nucleosomes by packaging DNA. The positive charge of the core histones causes the consistency of the chromatin and thereby regulates access by transcription factors (Adcock and Lee, 2006; Bayarsaihan, 2011). Histones and wrapped DNA in the condensed form of chromatin are tightly packed, thereby it is transcriptionally inactive. However, transcription factors could bind to DNA in the open chromatin and finally lead to gene expression. Addition or removal of acetyl groups to the core histones increases and decreases DNA accessibility, respectively and thus promotes transcription or silences gene expression (Marks et al. 2003). The acetylation and deacetylation of histones are known as reversible epigenetic mechanisms operating before transcription initiation (Hamon and Cossart, 2008).

Histone acetyltransferases (HATs) are enzymes that acetylate amino acids on histone proteins and histone deacetylases (HDACs) are a class of enzymes that remove acetyl groups. Fruit fly D. melanogaster have three of the four classes of HDACs that were reported in humans (Peleg et al., 2016). It has been shown that in the greater wax moth Galleria mellonella (Mukherjee et al., 2012) and in the flesh fly Sarcophaga bullata (Reynolds et al., 2016), there is a balanced upregulation of HATs and HDACs during insect metamorphosis. In G. mellonella larvae that were injected with HAT inhibitors (suberonylanilide hydroxamic acid) early transition to the pupal phase occurred. Interestingly, HDAC inhibitors (sodium butyrate) injection delayed pupation. As well as, in the honey bee A. mellifera sodium butyrate induced immunity and detoxification genes expression and increased resistance against insecticides (imidacloprid and the microsporidian) (Hu et al., 2017).

MicroRNAs

MicroRNAs (miRNAs) are non-protein coding small RNAs (18 to 25 nucleotide in length) that could epigenetically upregulate their target genes or silence them at the posttranscriptional level by either degradation of the target mRNA or inhibition of translation (Bartel, 2009). They inhibit the translation of specific mRNAs by base-pairing with the untranslated regions or occasionally in the coding region (Ambros, 2004; Bartel, 2004; Asgari, 2011). In general, miRNAs are evolutionarily conserved between different eukaryotic species and regulate a range of cellular processes, such as immunity, development, differentiation, and apoptosis (Bartel and Chen, 2004; Giraldez et al., 2005).

Many studies have documented that a single miRNA may control hundreds of different target genes and miRNAs may regulate more than 30% of animal genes (Bartel, 2009; Bushati and Cohen, 2007; Sato et al., 2011). In D. melanogaster seven miRNAs were identified that involved in the regulation of immune responses such as peptidoglycan receptor proteins (Fullaondo and Lee, 2012). Also, another miRNA from the fat body of this insect was known that control immunity-related gene translation (Choi and Hyun, 2012).

It is reported that bacterial and viral infections could change miRNAs expression levels in animals and plants (Fassi Fehri et al., 2010). Wolbachia pipientis is an obligate endosymbiont in a wide range of invertebrates, with the ability of host reproduction manipulation and alteration of host insect lifespan (Hussain et al., 2011). As well as, it could alter the miRNA profile of the mosquito, A. aegypti by induction of a host miRNA targets metalloprotease gene. Therefore, expression of the metalloprotease gene was induced after Wolbachia infection in cell lines and mosquitoes. Interestingly, inhibition of the miRNA decreased gene expression. Wolbachia endosymbiont manipulates the host metalloprotease gene via induction of cellular miRNA to replicate efficiently in the host (Hussain et al., 2011).

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Epigenetic interaction between insects and symbionts

Many studies have reported close associations of microbes with the insects, especially for Hemiptera and their mutualistic symbionts (Kim et al., 2016). Insect-microbe interactions can help insects by the production of a wide array of metabolic products that complement their metabolic needs (Hansen and Moran, 2014). There is a lot of interest in the epigenetic interaction between insects such as aphids and their beneficial symbionts (Kim et al., 2016).

Insect symbionts can influence DNA methylation patterns in insects and change gene expression in adaptive ways. For example, Ye et al. (2013) have reported that Wolbachia infection can change methylation and demethylation pattern of A. aegypti genome. Methylation has induced transcriptional silencing of 63 genes in A. aegypti, such as membranes and calcium ion transmembrane transport, however, phenotypic consequences were not clear. Demethylation was more common due to Wolbachia infection by affecting 699 genes (Ye et al., 2013).

DNA methylation is mediated by DNA methyltransferase enzyme and A. aegypti has only one DNA methyltransferase gene. Zhang et al. (2013) have reported Wolbachia infection of A. aegypti suppressed the expression of this gene and led to hypomethylation of the genome.

Host-parasite interactions: an intimate epigenetic relationship

Environmental signals affect intracellular signaling pathways that lead to changes in chromatin structure and epigenetic mechanisms that affect gene expression and cellular phenotypes (Berger et al., 2009). Intracellular pathogens can alter environmental states from inside the cell by hijacking host cell machinery and using a variety of strategies in order to survive and prosper (Cheeseman and Weitzman, 2015). Therefore, gene expression profiles are changed by parasite infection (Kinnaird et al., 2013; Sessions et al., 2013). This alteration of gene expression can drastically change cell phenotypes, including inflammatory responses and stress (Cheeseman and Weitzman, 2015). Since a host DNA sequence is intact, these phenotype changes are known as epigenetic.

A. aegypti and Anopheles gambiae, the mosquitoes that are known as vector insects, have interesting epigenetic. Because all mechanisms of epigenetic including histone acetylation/ deacetylation, miRNAs and DNA methylation can influence the susceptibility of these species to parasites; Hence, the success of transmission (Hussain et al., 2011; Ye et al., 2013; Sharakhov and Sharakhova, 2015).

Entomopathogens, microorganisms that are pathogenic to insects, can delay the development of infected host insects. For example, the injection of living spores of the parasitic fungus Metarhizium robertsi into last-instar Galleria mellonella larvae delays the pupal phase. Also, injection of specific HAT or HDAC inhibitors induced the same delay, thus it can suggest that parasites for epigenetically regulation of host gene expression before transcription, may use histone acetylation and deacetylation in the host insect (Mukherjee et al., 2012, 2015). To suppress the host immune response, pathogen control genes interfering with developmental delay, therefore, it seems that immunity-related genes and developmental delay are controlled by the same epigenetic mechanisms (Vilcinskas, 2016). In the model host, red flour beetle Tribolium castaneum, feeding with specific HAT or HDAC inhibitors affected development (Bingsohn et al., 2016).

Other studies have shown that virulent Listeria monocytogenes strains (Mukherjee et al. 2013) and entomopathogenic bacterium Serratia entomophila (Mukherjee et al., 2015) delay development of G. mellonella larvae by changing the expression of genes encoding HATs and HDACs.

Using this model insect it was documented that immune priming in insects can be mediated by the maternal transfer of bacteria from the gut into the developing eggs (Freitak et al., 2014), and this is associated with pathogen-mediated transgenerational epigenetic effects (Mukherjee et al., 2015).

Like other parasitic fungi, M. robertsii is able to communicate with host insect during infection. This fungus can sense the presence of antifungal peptides and host serine protease inhibitors induced during infection. Thus, the fungus upregulates chymotrypsin-like proteinases and metalloproteinases gene expression to degrade host protease inhibitors. This alteration of gene expression in the host and fungus is assumed as an epigenetic mechanism and accompanied by imbalanced expression of HATs and HDACs (Mukherjee and Vilcinskas, 2018). Parasitoids like ichneumonid or braconid wasps can also change host insect histone acetylation (Bae and Kim, 2009; Bitra et al., 2012; Song et al., 2008).

Entomopathogen Bacillus thuringiensis (Bt) has been used against coleopteran and lepidopteran insects like G. mellonella. There are increasing reports of insect's resistance to Bt. Interestingly, a shift in the balance between the expression of genes encoding HATs and HDACs results in the transcriptional reprogramming of immunity-related genes and resistance formation (Dubovskiy et al., 2016; Mukherjee et al., 2017). The pathogen can use this epigenetic mechanism to delay or even arrest host development (Vilcinskas, 2016).

Conclusions

In biology, phenotype diversity is an important issue because population adaptation to environment and success against all threats such as pathogens, toxins, etc. can be achieved by the evolution of biodiversity. Epigenetic is an important origin of biodiversity. Selection of mutations needs a long time. However, the presence of new phenotypes over short evolutionary timescales is due to epigenetics.

In general, many studies have reported that DNA methylation, histone acetylation/deacetylation, and small non-coding RNAs are associated with phenotypic diversities not only in insects but also in other organisms. However, it is difficult to prove how a special phenotype could be originated from a specific epigenetic basis or mechanism of inheritance across generations. More experiments need to be done and focus on these goals by studying social insects or insect cell lines.

Many studies have reported epigenetic phenomena in different insect species, but social insects and aphids are ideal for studying the role of epigenetic mechanisms due to having multiple phenotypes and different behavior that come from the same genome.

Epigenetic interaction between insects and symbionts is another interesting subject that unfortunately, there are not many studies about symbionts epigenetic. To the best of my knowledge, it has been reported just for one microbe called Wolbachia. There are not more epigenetic studies about other insect symbionts.

Nowadays, pesticide resistance is a global problem. Change of insect physiology or behavior can lead to resistance formation. These changes might come from epigenetic bases. Taken together, epigenetic studies in insects are not only progressing but also promising to find a solution for pesticide resistance formation.

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اپی ژنتیک در حشرات

اعظم امیری[1*]

چکیده

اپی ژنتیک در حشرات منبع مهم تنوع زیستی است که می تواند محرک های محیطی را به تغییرات فنوتیپی وراث پذیر و تنوع زیستی بدون جهش تبدیل کند و با تغییر سطوح بیان ژن مستقل از تغییرات توالی DNA است. اپی ژنتیک ممکن است نقش مهمی در پارامترهایی مانند نمو، طول عمر، تولید مثل، تنوع فنوتیپ های خاص جنسیتی، ایمنی و هر دو فرگشت برهم کنشهای حشره- گیاه و حشره- میکروب را داشته باشد. برای بررسی اساس مولکولی اپی ژنتیک، حشرات اجتماعی مانند مورچه ها یک سیستم آزمایشی طبیعی را ارائه می دهند. در حشرات اجتماعی، فنوتیپ های متعدد و انواع مختلفی از افراد از یک ژنوم واحد بوجود می آیند. وجود فنوتیپهای جایگزین که توسط همان ژنوم کدگذاری شده اند، به عنوان پلی فنیسم شناخته می شود. پلی فنیسم کاست از اطلاعات مولکولی حاصل می شود که پس از اینکه یک بار ایجاد شد، میتواند بعدا از طریق توارث اپی ژنتیک حفظ شود. هم چنین برهم کنشهای انگل- میزبان، روابط نزدیک اپی ژنتیکی است. مکانیسم های اپی ژنتیک حشرات به قبل از رونویسی و تنظیم ژن پس از رونویسی تقسیم می شوند. متیلاسیون DNA و استیلاسیون / داستیلاسیون هیستون قبل از رونویسی و RNA های کوچک غیر کدگذاری شناخته شده به عنوان microRNAs به عنوان تنظیمات ژن پس از رونویسی شناخته می شوند. متیلاسیون در سراسر ژنوم رایج است و به عنوان منشاء بیان متمایز ژن در کاست های حشرات اجتماعی گزارش شده است. به طور کلی، حشرات دارای نسبت کم سطح متیلاسیون DNA، در مقایسه با سیستم های پستانداران هستند. مطالعات اپی ژنتیکی در حشرات نه تنها در حال پیشرفت هستند، بلکه امید بخش هستند که راه حلی برای مقاومت در برابر آفت کش‌ها پیدا کنند.

واژگان کلیدی: حشره، اپی ژنتیک، پلی فنیسم، مقاومت، برهم کنشهای میزبان- انگل.

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