Neural basis of olfactory processing in social insects(社会性昆虫における嗅覚処理神経基盤の解析)

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論文内容の要旨

Olfaction mediates a variety of animal behaviors such as antipredetor avoidance behaviors, courtship behaviors, detection of food corruption and food searching behaviors, all of which are essential for survival of animals. The olfactory system processes chemical information in two separate channels, each of which deals with 1) infochemicals released by conspecifics that evoke stereotyped forms of behavior, such as female sex-pheromone that evokes specific orientation behavior in males or 2) environmental odorants, the value of which may be changed through experiences, such as odorants of nectar-providing flower species, which are learned by nectar-foraging insects such as honeybees. For a better understanding of olfaction, the commonalities and differences of neural mechanisms by which these two biologically distinct forms of olfactory information are processed need to be clarified.

To address this question, social insects are thought to be one of the best model species due to their sophisticated social organizations based on pheromone communication, their efficient foraging behaviors guided by olfaction, relatively simpler brain architectures, and relatively small number of neurons forming the brain, many of which are individually identifiable. Thus, in this thesis, I describe neural mechanisms underlying pheromonal and non-pheromone environmental odor processing in the brain of social insects.

In chapters I, II and III, I describe alarm pheromone processing in the brain of the ant *Camponotus obscuripes* based on results of intracellular recording and cell staining. In chapter I, it is shown that two alarm pheromone components in *C. obscuripes*, formic acid and *n*-undecane (Fujiwara-Tsujii et al., 2006), are processed in a specific cluster of glomeruli in the antennal lobe, which is the primary olfactory center of insects. In chapter II, a general schema of alarm pheromone processing in the brain of *C. obscuripes* is presented. I propose the presence of two parallel pathways to process alarm pheromone: one is intervened by the lateral horn and the other is intervened by the mushroom body, both of which are known to be higher olfactory centers. Since many of the mushroom body extrinsic neurons responded to alarm pheromones and other environmental odors and some of them even responded to other modalities of stimuli, pheromone information is integrated with information of other modalities in order to achieve pheromone-triggered, context-dependent behaviors relying on multisensory inputs, such as aggressive behaviors towards enemies, in the second pathway. In chapter III, I deal with the first pathway. I report that terminal boutons of alarm pheromone-sensitive projection neurons which have dendrites in one of the specialized glomeruli in the antennal lobe mainly occupy a small compartment in the lateral horn, while

those of pheromone-insensitive neurons are rarely seen in that compartment. Since a class of pheromone-sensitive output neurons from the lateral horn also had dendrites in this region, I propose that the compartment is specialized for alarm pheromone processing. Moreover, most of the pheromone-sensitive neurons were originated from one of the alarm pheromone-specific glomeruli in the antennal lobe, while pheromone-insensitive neurons were not. Processing channels from these glomeruli to the lateral horn region where pheromone-sensitive neurons converge are thought to play a major role in alarm pheromone processing in the ant brain.

In chapter IV, I present results obtained by using calcium imaging technique that reveal coding properties of olfactory responses at the terminal boutons of two classes of projection neurons, l-ACT and m-ACT neurons, in the calyx of the mushroom body of honeybees. I found that m-ACT boutons exhibited clear concentration dependency and greater response at a higher concentration, while l-ACT boutons exhibited odor-specific, complex concentration-dependencies with substantial inhibitions at a higher concentration. This difference is also reflected by the difference in odor mixture effects, i.e., l-ACT boutons tended to be inhibited when two odors were mixed, while m-ACT boutons tended to increase or showed no change in response. Since l-ACT boutons also tended to respond at lower concentrations, I conclude that the physiologically effective concentration range is broader and is shifted toward a lower concentration range in l-ACT boutons compared to m-ACT boutons. Moreover, I show individual bouton activities in axon branches revealed by combinatorial use of calcium imaging and 3D reconstruction of terminal branching patterns acquired by confocal microscopy.

Results of these studies will contribute to a further understanding of pheromonal and non-pheromonal odor processing in the brains of social insects.

論文審査結果の要旨

アリやミツバチなどの社会性昆虫では、嗅覚が高度に発達しており、その脳が比較的単純な構成を持つことと相まって、動物の脳における嗅覚情報処理の基本原理解明のための優れたモデル系となりうる。

山方恒宏は、まず、ムネアカオオアリを材料に、警報フェロモンの脳内処理様式について、脳のニューロンからの細胞内記録・染色を行って解析し、一次嗅覚中枢である触角葉に警報フェロモンに特異的に反応する糸球体群があることを初めて明らかにした。これらの糸球体に樹状突起をもつ投射ニューロンのほとんどは、警報フェロモンのみに特異的に反応し、一般臭には反応しなかった。

触角葉の嗅覚情報は、投射ニューロンによって前大脳に運ばれる。そこで次に、前大脳での警報フェロモン情報処理について、細胞内記録・染色法を用いて解析した結果、警報フェロモン情報は2次嗅覚中枢である側角とキノコ体に運ばれ、キノコ体では一般臭や嗅覚以外の感覚情報と統合されること、また前大脳には、側角やキノコ体などで処理した警報フェロモン情報を再統合し、行動に結びつける役割を担うニューロン群があることが明らかになった。

さらに、側角での警報フェロモン感受性投射ニューロンと非感受性投射ニューロンの終末突起の分布について解析した結果、側角には警報フェロモン処理に特化した小領域があることを明らかになった。

最後に、山方恒宏は、ミツバチ脳における一般臭の情報処理について解析した。ミツバチなどの昆虫では、触角葉からの投射ニューロンは、内側神経路と外側神経路の２つの神経路を構成し、それぞれの神経路の投射ニューロンは、側角やキノコ体において部分的に異なる領域に終末する。そこで、２つの神経路の投射ニューロンの間で嗅覚情報符号化様式に違いがある可能性について、カルシウムイメージング法を用いて調べた結果、２つの神経路の投射ニューロンには、匂い選択性、抑制応答の出現頻度、応答の濃度依存性、混合物への応答様式において明確な違いがあることが明らかになった。この発見は、２つの神経路の間に機能の違いがあることを初めて示唆したものである。

本研究は、山方恒宏が自立して研究活動を行うに必要な研究能力と学識を有することを示している。したがって山方恒宏提出の論文は、博士（生命科学）の博士論文として合格と認める。