PHEROMONE COMMUNICATION IN MOTHS AND BUTTERFLIES

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INTRODUCTION

Insects as well as many animals of other classes, use chemical signals - so called pheromones (Karlson and Lüscher, 1959; Karlson, 1960; Karlson and Butenandt, 1960) - for intraspecific communication. Our interest is to gain an understanding of communication in the form of exchange of biologically meaningful signals between conspecifics (Schneider, 1965; Wilson, 1970), in moths and butterflies. Originally it was assumed that pheromones are species-specific, that is, each species produced, for example, its own sexual attractant. While this appears to be true in many cases, recent investigations have shown that very often the situation is much more complex. Closely related species may have the same pheromone and therefore need additional means, for example differences in their diel rhythm, behavioral differences and/or different amounts of the attractant (Kaae et al., 1973), to secure their reproductive isolation. Furthermore, it has been found that many species use more than one compound to attract the sexual partner. In field experiments, the addition of other compounds to the main pheromone can increase the catching rate of one species and block the attraction of another. In some cases, two closely related species were found to utilize the same two isomers of an acetate in different ratios (Minks et al., 1973; Klun et al., 1973). To what extent interspecific attraction (but not necessarily mating attempt) occurs under normal field conditions is not known, but cross-attraction was observed in field experiments (Ganyard and Brady, 1972).

The state of the art with regard to pheromone biology in insects was recently reviewed in a number of articles and books: Butler, 1967,

PHEROMONE COMMUNICATION AND OLFACTORY RECEPTION IN MOTHS

The pheromone communication system in the moth as shown schematically in Fig. 1 illustrates the extent of our present understanding of the different functions involved. No attempt will be made here to present a complete picture, but rather to emphasize some functions and to present some examples.

Some time after emergence from the pupa, the virgin female moth expands her sexual attractant glands. The performance of this "calling" behavior (Fig. 2) depends upon a number of factors, some of which are known. As a rule, calling is only observed before copulation. In the female of the domesticated silkmoth *Bombyx*, calling is more or less continuous, while in most other moths studied to date, calling depends upon a diel rhythm which appears to be correlated with the activity rhythm of the male of this species (Bartell, 1968; Traynier, 1970; Shorey, 1973; Fatzinger, 1973). In the well studied cabbage looper moth (*Trichoplusia ni*), it was found that the duration of calling and the amount of attractant emitted depended upon the wind speed (Kaae and Shorey, 1972). This phenomenon can be understood in relation to the distribution of the luring odor (see below).

In some cases (for reference see Shorey, 1973), the female moths fly to the larval food plant before they start calling. A particularly striking food-plant odor dependency was reported for the North American Saturniid *Antheraea polyphemus* (Riddiford, 1967; Riddiford and Williams, 1967). The female of this moth only called in the presence of the odor of the preferred food plant: oak. The critical compound is t-2-hexenal, which is found in most green leaves. Pure hexenal brings about the same effect as oak leaves, while other leaves - in spite of the fact that they contain hexenal - do not induce calling. The odor signal is perceived with antennal receptors. With regard to the failure of leaves such as birch to elicit calling, one is led to assume that leaves of plants other than oak contain, in addition to the omnipresent hexenal, some other compounds which prevent calling. The experiments of Riddiford and Williams (1971) have enabled us to advance a tentative functional scheme on the basis of experiments with this and other species. (Fig. 3): The hexenal receptor cells activate neurosecretory brain cells, the axons of which run to the corpora cardiaca, where their neurosecretion subsequently activates local hormone cells. The latter produce a "calling hormone" which circulates in the hemolymph and is the prerequisite for expansion of