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INTRODUCTION

Pheromones as Tools for Olfactory Research

Thomas A. Christensen and Peter W. Sorensen[1]

Arizona Research Laboratories, Division of Neurobiology, University of Arizona, Tucson, AZ 85721 and [1]Department of Fisheries and Wildlife, University of Minnesota, St Paul, MN 55108, USA

Correspondence to be sent to: T.A. Christensen, Arizona Research Laboratories, Division of Neurobiology, 611 Gould-Simpson Building, Tucson, AZ 85721, USA

Abstract

We have long been fascinated by the unique ability of odors to stir our emotions and to evoke long-forgotten memories, but certain odors play a much more fundamental role in that they vastly improve an organism's chances for reproductive success and survival. These odorants are called pheromones, a term commonly applied to semiochemicals that are released by one member of a species and evoke a specific reaction or reactions from members of the same species. Pheromones are known for both the specificity and the potency of their actions, which can be behavioral and/or neuroendocrinological. Pheromones can stimulate individuals to aggregate, to disperse, or to react defensively in the presence of a predator, but they are probably best known for bringing the sexes together. Some pheromones have also been found to trigger a dramatic release of pituitary hormones in several vertebrate species. Although first identified in insects, more recent studies show that sex pheromones influence the lives of a wide range of organisms, from microbes to man. The hormonally-derived sex pheromones in teleost fish, and the airborne pheromones of moths are two systems that illustrate how scientists have used these specialized chemical signals as important tools to investigate the morphology, physiology and biochemistry of olfactory-receptor systems, the mechanisms of odor-information processing in the brain, and the diverse range of behaviors and endocrinological changes associated with pheromonal communication. While our focus is on these two animal models, other examples, including mammalian pheromone systems, are also discussed. **Chem. Senses 21: 241–243, 1996.**

Introduction

It is difficult for most people to imagine their world dominated by chemical senses, in which routine activities like recognizing one's friends and finding food depended on one's ability to discriminate emitted olfactory cues. In the words of E.O. Wilson (1963), 'The notion of such a communication system is of course strange because our outlook is shaped so strongly by our own peculiar auditory and visual conventions'. For many organisms, however, the use of olfactory cues is a critically important mode of communication. The exchange of chemical substances between individuals is often required for a wide range of social interactions, and the accurate discrimination of these signals may mean the difference between life and death. Among the most powerful chemical messengers of this type are the group of socially-relevant odorants commonly known as 'pheromones'. The various behavioral and endocrinological roles of pheromones, and their importance as tools in the study of olfaction were the subject of a symposium held in April 1995 at the Seventeenth Annual Meeting of the Association for Chemoreception Sciences in Sarasota, Florida. This Introduction and the three articles that follow, discuss the proceedings of this symposium, and illustrate how pheromones have been used to investigate numerous and varied aspects of olfaction, from peripheral mechanisms of detection, to the central processes of odor discrimination, to the expression of behavior.

Definitions

At the outset, it is important (especially for the uninitiated) to define a few terms that are often applied in the context of chemical communication. Odorants that convey information between organisms have, for more than 50 years, been grouped under the general terms 'semiochemicals' or 'ectohormones'. In 1959, Karlson and Lüscher drew a distinction between chemical substances that convey interspecific information (e.g. phagostimulants) and those that convey a specific message between members of the same species. For this latter group they coined the term 'pheromones' and defined them as 'substances which are secreted to the outside by an individual and received by a second individual of the same species, in which they release a specific reaction, for example, a definite behavior or a developmental process' (Karlson and Lüscher, 1959). Although there has been some doubt that this definition should be applied in its strictest sense to higher vertebrates (e.g. mammals; Beauchamp *et al.*, 1976), we believe that the original intent of the term was simply to help describe those socially-active odorants that evoke specific reactions and greatly improve an organism's chances for reproductive success and survival (see Sorensen, 1992, 1996, this issue). Thus, the key to defining a substance (or mixture of substances) as a pheromone lies in this criterion, and not, as Karlson and Lüscher themselves point out, in the requirement for strict species specificity. This point is perhaps best illustrated by the well-defined pheromonal systems of many insect species (Birch and Haynes, 1982; Payne *et al.*, 1986; Schneider, 1992; Cardé and Minks, 1996). It is now clear, for example, that several species of moths use exactly the same compounds in their sexual lures, and that species specificity comes about as a result of varying the *ratio* of the compounds emitted from the female pheromone gland (Arn *et al.*, 1992), as well as a selective responsiveness of the male's olfactory system to these odorants (see Mustaparta, 1996, this issue). In this manner, relatively few odorants can form the chemical substrate for many possible species-specific blend combinations (see Kaissling, 1996, this issue). A similar scenario appears to operate for the hormonally-derived sex pheromones in teleost fishes, and recent findings now indicate that some mammals may employ pheromonal mixtures (see Sorensen, 1996, this issue).

Pheromones and their influence on behavior

Pheromones have also been useful in helping us understand the fundamental chemical and physical properties of olfactory stimuli in the environment. Aside from the knowledge that insect pheromones are typically mixtures of odorants, it is important to note that individual odorants that comprise the pheromone blend may have more than one biological function. For example, one odorant may act as a component of an attractant sex-pheromone in one species, while at the same time, cause the aversion of males of a sympatric species, in which case it would function as an 'allomone' (see Christensen and Hildebrand, 1994, and references therein). Thus, a given semiochemical can only be described as a pheromone in the context of the particular specific response that it evokes (Birch and Haynes, 1982).

Pheromones have wide-ranging effects in a variety of different organisms. If the pheromone produces a more or less immediate effect on behavior, it is said to have a 'releaser' effect (Wilson and Bossert, 1963). The best known examples of releaser pheromones are those that evoke sexual attraction, but releaser pheromones can also evoke defensive postures or dispersal in the presence of a predator, and the trail-following pheromones of social insects are examples of releasers that evoke a recruitment response (reviewed in Wilson, 1963). If, on the other hand, a pheromone triggers a physiological chain of events that leads to a change in physiology or an eventual change in behavior, it is said to have a 'primer' effect. Examples of primer pheromones are ones that result in hormone secretion, which in turn may influence mechanisms such as ovulation and sperm production. In some instances (such as the pre-ovulatory pheromone in goldfish) pheromonal actions may be complex, and the pheromone may function as both a primer and as a releaser (Sorensen, 1992, 1996, this issue; Stacey *et al.*, 1994). Through the study of these releaser and primer effects in both vertebrates and invertebrates, we have come to realize several important characteristics of pheromonal systems that provide us with key insights into general olfactory processes.

The participants

In this symposium, our aim was to illustrate how pheromones have been useful tools in helping to elucidate some of today's fundamental questions in olfactory research. In his article, Peter Sorensen discusses the importance of careful behavioral observations in order to fully appreciate the role of pheromones in promoting species isolation, and explores the neural bases of such behaviors. Karl-Ernst Kaissling then discusses how the identification of pheromones as behaviorally-relevant stimuli has led to an increased understanding of the mechanisms underlying the anatomy, physiology and biochemistry of olfactory-receptor systems in insects. Finally, Hanna Mustaparta reviews some of the mechanisms underlying the first-order processing of pheromonal information in the brain. We hope that these articles will serve as useful illustrations of how different researchers have employed pheromones in both 'bottom up' and 'top down' approaches to understanding the physiological mechanisms underlying odor discrimination in living organisms.

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