Advances in THE STUDY OF BEHAVIOR

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Odor Processing in Honeybees: Is the Whole Equal to, More Than, or Different from the Sum of Its Parts?

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I. INTRODUCTION

Processing and learning compound stimuli is an important biological problem.¹ Every organism, in nearly every environment, is faced with a continual, multifaceted stream of stimuli that may be related to specific effects or outcomes. How do animals process compound stimuli under such circumstances? Do they treat the components separately and associate them with a common outcome? Do they treat the compound stimulus as an entity that is drastically different from its components and associate this entity with a specific outcome? These questions reveal useful ways of thinking about how animals may process and respond to a compound stimulus, and they correspond to the following general question: What mechanisms govern the integration of that stream of events and how are these events represented in the nervous system? The answer to these

¹ We use the term “compound stimulus” in the sense of a stimulus composed of two or more elements without making assumptions about the way in which the nervous system treats such a stimulus. The term nevertheless refers to a psychological perspective and thus to the question of how this kind of stimulus is processed.
questions may be provided by a combined approach in which Pavlovian conditioning, one of the oldest and most systematically studied phenomena in psychology, and neurobiological investigations on stimulus processing in model systems converge into a common strategy.

In the present review, we describe studies of compound stimulus processing and learning that have focused on olfactory learning in an invertebrate, the honeybee *Apis mellifera*. Honeybees are a traditional model for studying learning and memory (Giurfa, 2003; Menzel, 1999, 2001; Menzel and Giurfa, 2001). Olfactory learning in bees has been well characterized and follows the Pavlovian conditioning scheme (Bitterman et al., 1983). Here we describe a series of conditioning experiments and derive conclusions on how bees treat olfactory compound stimuli. Since the neural pathways underlying olfactory learning in the bee brain are relatively well known (Menzel, 1999, 2001), we are able to interpret our findings from a neurobiological perspective in which we correlate our behavioral findings with findings on neural coding of olfactory compound stimuli in the olfactory neuropils of the bee brain. Our review may be taken as an advertising campaign for interdisciplinary studies in which approaches from experimental psychology (Pavlovian conditioning as a research tool in behavioral biology) and neurobiology (optophysiological studies on olfactory coding as a research tool in sensory neuroscience) are combined.

II. PAVLOVIAN CONDITIONING AND MODELS OF COMPOUND STIMULUS PROCESSING

As early as 1897, the Russian physiologist Pavlov noted that, in dogs, stimuli preceding the appearance of food (e.g., the smell of food) elicited what he called “psychic” salivary secretion (Pavlov, 1902), or a conditional reflex. His empirical and theoretical elaboration of these “psychic” secretions and of cortical function founded a scientific endeavor distinguished by objective terminology, well-defined procedures, and empirically driven theoretical concepts (for an overview see Gormezano and Moore, 1969). Pavlov, working within the reflex tradition of physiology and early behaviorism, saw conditioning as a kind of low-level mechanical process in which control over responding is passed from one stimulus to another. However, in the late 1960s and early 1970s, after the “cognitive revolution,” conceptualization and knowledge of the associative processes underlying Pavlovian conditioning changed and expanded dramatically (see, e.g., Rescorla, 1988). Nowadays, Pavlovian conditioning deals with the mechanisms that enable organisms to represent the structure of their world, especially the relationships between environmental events. This new view may be traced back to the associative tradition originating in philosophy (see Lachnit, 2003). This combination of properties, especially the fact that research in Pavlovian conditioning (1) allows for precise manipulations of independent variables and is primarily driven by (2) experimental designs and (3) explicit—in part formalized—theories, encouraged us to take advantage of this approach in the study of olfactory processing in honeybees.

Let us now focus on the initial question from a theoretical viewpoint, namely, which mechanisms govern the integration of the stream of incoming events in compound stimulus processing and how are these events represented in the neural system? Three main positions should be distinguished, and these also lay the foundation for rival theories of associative learning. First, an elemental perspective, assuming that the whole (compound stimulus) equals the sum of its parts (elements). Second, the idea that the whole is more than the sum of its parts. And last but not least, the assumption that the whole is (totally) different from the sum of its parts, a point of view that is typical of the so-called configural approaches.

In Pavlovian conditioning many well-known effects have long been successfully explained in an elemental manner (Wagner, 1971), assuming that stimulus components are represented as separate entities and that the overall associative strength of a compound stimulus is based on the algebraic sum of the associative strength of its components (Rescorla and Wagner, 1972). If a compound stimulus AB consisting of the elements A and B is paired with an unconditioned stimulus (US), it is assumed that each element enters into a separate association with the US. This elemental summation principle, incorporated into many theories of associative learning (e.g., Mackintosh, 1975; Pearce and Hall, 1980; Rescorla and Wagner, 1972; Wagner, 1981), has important consequences. On the one hand, it may serve as a convenient but nevertheless powerful modular design principle for dealing with complex environmental events. The total associative strength of such an event is distributed among several components. In some situations this strength may be equally distributed, in others rather unequally, among the different components. On the other hand, when two separately trained stimuli are presented together, response to this compound stimulus will be more pronounced than to either element alone, a phenomenon that is called summation (Rescorla and Wagner, 1972).

There is, however, considerable evidence that animals are able to successfully handle discrimination problems that cannot be solved in a purely elemental manner. In such nonlinear discriminations, the associative strength of a compound stimulus does not result from the simple sum of the elemental associative strengths. An example of this kind of discrimination is negative patterning (e.g., Rescorla, 1972; Whithall and Wagner, 1972). In negative patterning, two stimuli are always reinforced when they are
presented on their own (A+, B+), but never when they are presented together as a compound stimulus (AB−). Another nonlinear discrimination problem is biconditional discrimination (Saavedra, 1975). In this discrimination problem, animals learn to discriminate two reinforced (AB+, CD+) from two nonreinforced (BC−, AD−) compound stimuli consisting of pairs of two out of four elements A, B, C, and D. In both discrimination problems, each element is reinforced and nonreinforced equally often so that the elemental summation principle incorrectly predicts intermediate levels of response to each compound stimulus. Animals are nevertheless able to both show anticipatory response to stimuli that are followed by an outcome, and to refrain from responding to stimuli that are not followed by an outcome. Solving these discrimination tasks implies that nonelemental processing of compound stimuli is possible.

One of the simplest ways in which associative theories could allow for this would be to assume that stimulus components are always encoded elementally but that, in addition, configurations of those components may also be encoded. Such configural units might be treated as additional “elements” (Rescorla, 1972, 1973; Whithlow and Wagner, 1972). In other words, the joint presentation of elements in a compound stimulus would result in an additional unique cue, which would be specific to those elements and that could by itself be associated with a specific outcome. According to such a view, the overall associative strength of a compound stimulus (e.g., AB) is based on the summed associative strength of its elements plus the associative strength of the unique cue. By postulating the existence of such an additional unique cue, elemental models can successfully handle the acquisition of discrimination problems such as negative patterning or biconditional discrimination. Negative patterning (A+, B+, AB−), for example, can be explained by assuming that A and B will both develop excitatory associations to the outcome and that their unique cue will develop an inhibitory association with this outcome. When A or B is presented alone, each will be able to activate a representation of the outcome so that a conditioned response will be elicited. When A and B are presented together, however, their joint presence will activate the unique cue, which then compensates for the excitatory properties of the elements due to its inhibitory associative status. The unique cue model can be viewed as an extension of elemental models, one that allows for a large degree of nonelemental processing, but at the same time keeps the gist of elemental models, that is, the summation of elements. In this view, the whole is more than the sum of its parts.

Configural models of compound stimulus processing propose another view of nonelemental processing. Some authors have suggested that compound stimuli are always processed configurally. The strongest view on how such a configural representation might be formed is that a compound stimulus is an entity that is distinct from its elements and that it is this entity alone that enters into an association with the outcome. This means that a compound stimulus that consists of two components, say A and B, is processed and represented with no relation to its components but instead as an independent configuration, which we shall call G. This would be a purely configural view (for a review see Kehoe and Gormezano, 1980). A less extreme, and in the area of associative learning empirically far more successful position, however, assumes that stimuli are processed configurally but that generalization takes place between the compound stimulus and the elements. According to the most prominent configural theory that has been put forward (Pearce, 1987, 1994, 2002), the degree of generalization between two stimuli is based on their component similarity, that is, on the number of elements they share. Thereby, part of the associative strength of a compound stimulus generalizes to its elements and vice versa (e.g., there will be reciprocal generalization between AB and A as well as between AB and B, but not between A and B).

In the following section we illustrate how it is possible to decide between these different models by choosing a model system, the honeybee Apis mellifera, which has allowed us to design Pavlovian conditioning experiments using olfactory compound stimuli.

III. Olfactory Pavlovian Conditioning and Olfactory Compound Stimulus Processing in the Honeybee

Honeybees can learn to associate odor stimuli with a sucrose solution reward. Such an association is biologically relevant, since it allows the bee to learn that a particular flower species, characterized by a specific odor, is profitable and can be exploited because it yields a nectar reward essential for the survival of the individual and the colony as a whole. Olfactory learning in honeybees can be studied and reproduced in the laboratory under controlled conditions by using the paradigm of olfactory conditioning of the proboscis extension reflex (PER) (Bitterman et al., 1983; Takeda, 1961). In this paradigm, hungry, harnessed honeybees are presented with olfactory stimuli associated with a reward of sucrose solution (see Fig. 1).

When the antennae of a hungry bee are touched with sucrose solution, the animal reflexively extends its proboscis to reach out to and suck the sucrose. Odors to the antennae do not usually release such a reflex in naive animals. If an odor is presented immediately before sucrose solution (forward pairing), an association is formed such that the mere presentation of the odor will subsequently release the PER in a following test. This
effect is clearly associative and involves classic conditioning (Bitterman et al., 1983). Thus the odor can be viewed as the conditioned stimulus (CS) and sucrose solution as an excitatory unconditioned stimulus (US).

Using this paradigm it is possible to ask how bees process and learn olfactory compound stimuli, odor mixtures (Chandra and Smith, 1998; Deisig et al., 2001, 2002, 2003). Early results indicated that bees could solve nonelemental olfactory discriminations such as negative patterning (Deisig et al., 2001) and biconditional discrimination (Chandra and Smith, 1998; Hellstern et al., 1995). This finding allows us to dismiss a purely elemental approach as an explanation for odor processing in honeybees. In the case of negative patterning, for instance, an elemental approach predicts that if the odors A and B were rewarded, bees should react considerably more to the mixture stimulus than to each of the elements. Thus the fact that bees learn to extend their proboscis to the single odors but not the compound stimulus (see Fig. 2) cannot be explained from this perspective. In further experiments dealing with odor processing in honeybees (Deisig et al., 2002) we found a certain amount of generalization between elements and the mixture stimuli, a fact that also allows us to dismiss the extreme configurational interpretation of odor processing. Clearly, if a mixture stimulus is an entity that differs drastically from its components, no generalization should occur. In addition, in these experiments we were able to show that a reduction of similarity between a mixture stimulus and the elements enhances the degree to which bees discriminate between both kinds of CS (Deisig et al., 2002). Discrimination was best in a CD versus A+ task (no sharing between compound stimulus and elements), intermediate in an AC versus A+ task (one out of two elements shared), and lowest in an AB versus A+, B+ task (two out of two elements shared). Solving the last task replicates the finding that bees can solve a negative patterning discrimination in the olfactory domain (Deisig et al., 2001) and allows us to again dismiss purely elemental interpretations of compound stimulus processing. Conversely, both the unique cue and Pearce’s configural theories can account for the acquisition of these three tasks.

Furthermore, bees trained with the A+, B+ versus AB− discrimination, and then tested with a novel mixture stimulus BC after training, showed a stronger response to BC than to B+. This finding is in contradiction to Pearce’s configural theory (for more details, see Deisig et al., 2002), which
would predict a decrement in responding due to generalization from B to BC.

Although our results so far suggest that olfactory mixture stimulus processing in bees relies on the use of unique cues, we reconsidered this suggestion on the basis of two main lines of evidence. On the one hand, results from other species (e.g., pigeons, rabbits) support the idea that—as is the case with odor mixtures—compound stimuli consisting of elements in the same modality favor the emergence of configural rather than of elemental associations (e.g., Pearce and Redhead, 1993; Pearce et al., 1997; Redhead and Pearce, 1995; Rescorla and Coldwell, 1995), whereas compound stimuli consisting of elements in different modalities favor the emergence of elemental associations (e.g., Bahkekapili, 1997; Myers et al., 2001). These findings would therefore predict that olfactory mixtures are treated as a configural entity and not as the sum of their elements plus a given unique cue. On the other hand, in the studies reviewed so far, we neglected the problem that in olfactory PER conditioning of honeybees the conditionability of odorants might be reduced because of interference between the components in an olfactory mixture. Neither the unique cue theory nor Pearce’s configural theory takes into account such interference. Hence, we additionally considered a modification of the unique cue theory initially suggested by Redhead and Pearce (1995). This modified unique cue theory predicts that conditioning a single reinforced element progresses in the manner predicted by the Rescorla–Wagner theory (Rescorla and Wagner, 1972), but in the case of compound stimulus trials it states that the presence of one element restricts learning about the other, thus yielding a slower rate of learning for the compound stimulus. Interestingly, it can be shown that our findings reviewed up to now (Deisig et al., 2001, 2002) are consistent with this modified unique cue theory.

Hence, in order to further decide between the unique cue theory, the modified unique cue theory, and Pearce’s configural theory, we confronted the bees with an A+, BC+, ABC− discrimination task, which requires them to learn three different stimuli (single odorants, binary and ternary odor mixture stimuli). Redhead and Pearce (1995) used this task successfully in a study on visual conditioning in pigeons to discriminate between different theoretical possibilities for compound stimulus processing. The task allows one to decide between the rival theories for the following reasons (for further details see Deisig et al., 2003): the unique cue theory expects a better differentiation between BC+ and ABC− than between A+ and ABC− because of summation of the associative strengths of B and C on binary compound stimulus presentation. Conversely, both Pearce’s configural theory and the modified unique cue theory predict better differentiation between A+ and ABC− than between BC+ and ABC−. For Pearce’s configural theory this is due to the higher degree of generalization between the BC+ and the ABC− compound stimuli (two elements, B and C, in common), which renders this discrimination difficult. For the modified unique cue theory the presence of one stimulus restricts learning about the other in reinforced compound stimulus trials (BC+) and this results in a slower rate of conditioning for this compound stimulus. Furthermore, the modified unique cue theory and Pearce’s configural theory differ in their prediction of summation at the beginning of training. According to the configural theory no summation should occur on compound stimulus presentation, while the modified unique cue theory predicts summation. Thus, on the basis of empirical results, the A+, BC+, ABC− design enables us to decide between the three theories.

Deisig et al. (2003) showed that bees differentiated faster between the reinforced single odor A+ and the nonreinforced ternary mixture stimulus ABC− than between the reinforced binary mixture stimulus BC+ and the nonreinforced ternary mixture stimulus ABC− (see Fig. 3). Thus, the outcome of the experiment clearly rejected the predictions of the unique cue theory, but was consistent with the predictions of the modified
unique cue and Pearce’s configural theory. Focusing on summation at the outset of training, in the first block of training we found that responses to ABC− were significantly stronger than those to A+ and BC+. This finding clearly supports the modified unique cue theory, but contradicts Pearce’s configural theory (see also Rescorla, 1997).

Taken together, all of our results reported so far are in accordance with a modified unique cue approach, which incorporates a correction for the reduced salience of components in a compound stimulus (in our case odor mixture stimuli) due to interference between them (James and Wagner, 1980; Mackintosh, 1971). Such interference might be related to the fact that the associative strength is limited such that all CS must compete for it (Revskey, 1971) or it might be related to limited attentional capacity. Paying attention to one CS will decrease the attention to, and learning about, another stimulus (e.g., Sutherland and Mackintosh, 1971). Last but not least, interference could occur at the sensory and neural level (e.g., odors competing for the same receptor type, or at a more central level, odors eliciting competing neural representations) or may be due to a storage problem (e.g., stimuli might compete for the maintenance of information in short-term memory even if they are easily perceived independently; see Atkinson and Shiffrin, 1968; Norman, 1968; Wagner, 1976).

IV. PHYSIOLOGICAL CORRELATES OF ODOR PROCESSING AND \textit{ELEMENT/COMPOUND INTERACTIONS}

In general, odors as used in the studies described above are received by chemoreceptors, in the bee antennae, that are localized in groups of 20–30 within a particular type of sensilla (sensilla placodea). Several hundred of such placodes are distributed over each antenna, and are particularly dense at its tip. The receptors have broad and overlapping response profiles, indicating that odor identity must be extracted from the combination of multiple parallel receptor inputs (Akers and Getz, 1993; Getz and Akers, 1994; Vareschi, 1971). Stronger odors elicit higher spike activity in each receptor cell and activate more receptor cells. However, odors also compete at the peripheral level for receptor sites or inhibit each other—possibly via different receptor molecules connected to antagonizing second-messenger pathways. Extracellular recordings from honeybee placodes revealed in some cases only the same or even fewer responses to binary olfactory mixtures as compared with single odorants (Getz and Akers, 1995). Model calculations indicated that antagonistic second-messenger pathways may lead to such competition and inhibition in the chemoreceptors (Malaka et al., 1995). However, the assumption that one chemoreceptor expresses more than one chemoreceptor molecule is not in accordance with the current view as derived from molecular genetic results in Drosophila (Vosshall et al., 1999). In any case, it is possible that already in the periphery both cooperative and antagonizing phenomena may lead to a deviation from simple additive superposition of odor-induced activity when olfactory mixtures are used. Further studies are needed to determine to what extent nonlinearity and interference occur at a peripheral level in the case of olfactory stimulus compounds.

At the central level, olfactory information is first processed in the antennal lobe, the primary olfactory neuropil of the insect brain. Odors are coded here by multiple activity patterns of glomeruli, the structural elements of the antennal lobe. Each of the 160 glomeruli in the bee antennal lobe is likely to receive input from only one receptor type. This assumption is made on the basis of findings in Drosophila, where molecular genetic experiments revealed that similar receptor genes are expressed in the receptor axons reaching the same glomerulus (Vosshall et al., 1999). Thus the antennal lobe can be considered as a landscape with receptor-specific locations (glomeruli) that are activated in combinations according to the rules defined by the overlap of the respective response profiles and the peripheral processing (Joerges et al., 1997). Intense synaptic processing occurs within and between the glomeruli. Local interneurons (approximately 4000) that are predominantly inhibitory, and projection neurons (approximately 800) conveying information to the higher order processing centers, the mushroom bodies, are the structural components in this network. Intracellular recordings from these elements revealed complex response patterns indicative of nonlinear processing that sharpens the response profiles, makes them less dependent on odor intensity, and leads to mixture-specific activation patterns of the output neurons (projection neurons) (Abel et al., 2001; Müller et al., 2002; Sachse and Galizia, 2002). These mixture-specific activations are of concern here because the rules behind the combination of activity patterns induced by the elements govern how odor mixtures are coded and learned.

The working of the antennal lobe network can be studied most effectively by optical imaging techniques. In these studies Ca²⁺-sensitive dyes are infused into either the whole network or selectively into specific components (e.g., single or multiple projection neurons), and neuronal activity is read from the Ca²⁺-dependent fluorescence signal when the antennae are stimulated with odor (Galizia et al., 1997; Joerges et al., 1997). Since an atlas exists for the bee antennal lobe, thus allowing identification of each glomerulus in recordings from different animals (Galizia et al., 1999), it is possible to establish the combinatorial physiological activity code for a
large number of odors (Sachse et al., 1999) and their mixtures (Joerges et al., 1997; see Fig. 4).

For the question considered in this article, it is relevant to know how olfactory mixtures are encoded at the level of the antennal lobe and to relate these results to the rival theories on compound processing. An important finding in this context is that activity patterns induced by mixtures of odors deviate more or less from the patterns that would be expected if simple linear superposition of the patterns elicited by the single odors governed neural processing (Joerges et al., 1997). Both the kind and the number of odors mixed together appear to play a role. Binary mixtures, for example, sometimes evoke patterns of glomerular activation that correspond to the simple addition of the patterns of the constituent odorants but that sometimes also differ strongly from the pattern expected from such a linear addition. Ternary or even higher order olfactory mixtures always deviate strongly from the expected pattern (see Fig. 5; Joerges et al., 1997; Sachse and Galizia, 2002).

The reason for such odor-specific suppression phenomena lies in the intrinsic organization of the antennal lobe networks. Two inhibitory networks can be found at the level of the local interneurons connecting glomeruli (see Fig. 5): a GABA-A receptor-dependent network and a histaminergic network (Sachse and Galizia, 2002). The first provides a widespread and more general inhibition, whereas the latter would be responsible for more localized specific inhibition. It is thus to be expected that the quality of the single odors—as reflected in their corresponding glomerular activity patterns and the number of odors in a mixture—should influence the recognition and possibly also the learning of the mixture. Nonlinear and inhibitory interactions within the antennal network, therefore, make the olfactory code of the olfactory mixture unique with respect to its constituting odors. Generalization between single odors and the mixture will depend on the amount of overlap between their activity patterns. In concluding this, we have therefore to refer processing of olfactory mixtures in the antennal lobe to the unique cue and the modified unique cue approaches postulated for compound stimulus processing. It is worth recalling at this stage that behavioral experiments supported the latter approach.

The second processing stage in the insect olfactory pathway is constituted by the mushroom bodies, which are involved in olfactory learning phenomena, and play a particularly important role in the olfactory memory trace (Menzel, 2001; Menzel and Giurfa, 2001). It is in these structures that the multitude of sensory modalities converge, and where context-dependence, across-modality configuration and comparison with remote memories (both acquired and innate) may be performed (Menzel and...
Fig. 4. Activity pattern of glomeruli in the antennal lobe of the bee when stimulated with 37 different odors. High activity as measured optophysiological is indicated by red/dark colors. Top left: Schematic representation of the antennal lobe with the numbers of the glomeruli measured with the optophysiological technique (see text). The 13 pictures (top right) show the activity patterns of different olfactory stimuli ranging from single odors, mixtures of two or three compounds, or mixtures composed of many compounds such as in the case of floral odors (Cit, citral; Ger, geraniol; Iso, isovalerate; PfM, peppermint oil; Org, orange; Car, carnation; Lnd, lime blossom, Lim, limonene; Cin, cineol; Eug, eugenol; Lio, linalool; Ment, menthol; Cio, d-limonellol. Bottom left: Twenty-four activity patterns showing
Kenyon cells with complex patterns of thousands of small activation spots (called microglomeruli) (Faber and Menzel, 2001; Szyszka et al., 2002). These patterns are odor specific, representing another odor-coding spatial code, but one now based on a large number of microglomeruli. At the output side of the mushroom body, neurons connect the mushroom body with descending neurons acting as premotor neurons, and with neurons that project back to its input side. These recurrent neurons are thought to provide an inhibitory feedback, since they are immunoreactive to GABA (Ganeshina and Menzel, 2001). Both types of output neurons show associative plasticity in odor conditioning experiments (Grünewald, 1999; Mauelshagen, 1993).

V. FUNCTIONAL MODEL OF THE OLFACTORY SYSTEM AS A NEURAL SUBSTRATE FOR ELEMENTAL AND COMPOUND PROCESSING

Next we shall ask whether the results reported above on elementary versus configural learning can be compiled into a functional model of the olfactory system of the honeybee that takes into account these data from the neuron-anatomical, electro- and optophysiological measurements. An additional piece of evidence is important in this context, namely the finding that the olfactory memory trace is distributed between the antennal lobes and the mushroom bodies. Each structure is able to form its own associative memory, and they can in turn control learned behavior independently of each other (Hammer and Menzel, 1998). So far, it is not known how these parallel memories may differ. We shall propose here that the memory trace formed in the antennal lobe results only from elemental associations, but that of the mushroom body includes mixture processing as a substrate for configural associations. Support for this view comes from Malun et al. (2002), who showed that an elemental discrimination (A+, B−) could be learned by bees with a single antenna and with mushroom body lesions (but intact antennal lobe) on the side of the stimulated antenna. In addition, Komischke et al. (2003) found that a positive patterning task (A−, B−, AB+) can be learned by a bee with a single antenna, but a negative patterning task only with both antennae. Since there are practically no connections between the two antennal lobes, but strong connections between the two sides of the brain at the level of the mushroom bodies, one may assume that only the stimulation of both antennae involves the mushroom bodies such that their contribution to olfactory coding and learning is normal.

Figure 6 summarizes the structure of our model. The odors A and B are the elements of AB, the mixture stimulus used for olfactory stimulation (level I). At level II, these odors are coded in the antennal lobe (AL) in the

Giurfa, 2001). Odor learning leads to synaptic plasticity both at the input and the output side of this neuropil (Mauelshagen, 1993). At the input side the information from the antennal lobe, via the projection neurons, reaches the intrinsic neurons of the mushroom body, the Kenyon cells. Since each projection neuron contacts many Kenyon cells, the combinatorial activity representing an odor is distributed over a large part of each mushroom body. Indeed, imaging experiments document large fields of activation in the activity patterns of alkanes (first row), primary alcohols (second row), aldehydes (third row), and secondary ketones (fourth row). The number of carbon atoms in each of these four chemical classes is indicated above each column (C-5 to C-10). Bottom right: Images as they appear in the microscope for the four respective odors in the C-10 column. Adapted from data published by Sachse et al. (1999) and Galizia et al. (1999). (See Color Insert.)
Fig. 6. Model of the olfactory pathway in the honeybee as it may apply for the elemental and configural forms of learning. Seven levels of integration are indicated (right) and correspond to the following processes: I, elemental odors A, B, and the mixture AB, a binary compound stimulus of the elements; II, odor coding at the level of the antennal lobe. Odors are represented as combinatorial codes of glomerular activity. Glomeruli 3, 4, and 5 are considered to inhibit glomerulus 2 (shaded gray). This inhibition is uncovered when the compound stimulus AB is used as a stimulus. It is assumed that each glomerulus can be associated with the outcome of the behavior (elemental associations), and will be able to control learned behavior at an elemental level; III, projection neurons (PN) transmit the information from the antennal lobe to the mushroom bodies. Their activity is displayed in the height of the vertical bars. Each odor is represented as an overlapping across-fiber activity pattern; IV, the first neural representation in the form of the PN across-fiber pattern provides the input to the second stage (central processing, Z) of neural integration in the mushroom bodies; V, here the input signals are classified (Z_A, Z_B, and Z_{AB}). Because of generalization processes the elements A and B will also activate the compound representation. These generalization processes are believed to be adaptive and learning dependent (see text); VI, the classified representations are associated with behavioral outcome; VII, learned behavior is a joint function of the integration processes at both the antennal lobe level (II) and the level of the mushroom body (VI).

The result of the odor processing in the antennal lobe is transmitted via the projection neurons (PN) in the form of an across-fiber activity pattern that carries the features of the neural representation at the sensory integration level (level IV: first neural representation). These distributed and combinatorial activity patterns (boxed A, B, and AB in Fig. 6) provide the input to the central integration level in the mushroom bodies (Z level). This input carries the information for both the elements and the compound stimulus. At the Z level (mushroom bodies, level V in Fig. 6) the stimuli are categorized and form the second level of representation (Z_A, Z_B, and Z_{AB}), now including a specific representation of the mixture stimulus AB. Models about the function of the mushroom body assume that the high neuroanatomical divergence between the input (PN) and the intrinsic fibers (Kenyon cells) together with a neural strategy of sparse coding may lead to representations in single neurons or small clusters of few neurons that are selectively activated by very specific combinations of particular odors or odor mixtures at their particular intensities (Heisenberg, 2003; Laurent, 2003). Consequently the mixture stimulus AB will activate not only the central representation of the compound stimulus AB, Z_{AB}, but also in part those of the elements (Z_A and Z_B). To reduce generalization between the compound stimulus and the elements one may assume specific inhibition between Z_{AB} and the elements' inputs (boxed A and B in Fig. 6). This specific inhibition can be provided by the recurrent neurons mentioned above that read out the categorization processes within the mushroom body that lead to the unique cue representation of the compound stimulus. Since these neurons are plastic in an associative manner they could make their recurrent inhibition dependent on former experience. As a consequence Z_A and Z_B will be reduced relative to the activation of Z_{AB}.
$Z_A$, $Z_B$, and $Z_{AB}$ are associated with their respective outcomes leading to the second and independent olfactory memory trace in the mushroom bodies (see Fig. 6, level VI). This trace now includes a specific code for the unique cue resulting from the mixture stimulus now represented as a compound stimulus, and thus will support nonelemental forms of learning. Optical imaging during olfactory learning indicated in addition that Kenyon cells change their response properties not only to the reinforced stimulus but also to the nonreinforced stimulus (Grünewald, 1999). $Z_A$, $Z_B$, and $Z_{AB}$ are thus represented as stored traces in the mushroom body. The amount of cross-talk between the learned $Z_A$, $Z_B$, and $Z_{AB}$ will depend on recurrent inhibition induced by $Z_{AB}$ and thus should depend on schedules of training since generalization strongly depends on the kind of training.

As pointed out above, the A+, BC+, ABC− discrimination task allows testing which of the three theories discussed here might apply to olfactory compound stimulus learning in bees. It was found that the data are consistent with a modified unique cue theory (Deisig et al., 2003) because summation was found at the outset of training (i.e., responses to ABC− were significantly stronger than those to A+ and BC+ in the first block of training; see Fig. 3). One can account for this finding by assuming that, initially during training, behavior is more strongly controlled by the contribution of the antennal lobe, where the summation of elemental associations dominates. Later, when learning progresses and the recurrent inhibitory properties in the mushroom bodies develop, the unique cue-controlled associations control behavior more strongly. Such a view is supported by the results of experiments with free-flying bees trained with color compound stimuli in which a short training results in elemental associations while longer training results in nonelemental associations (Giurfa et al., 2003).

Our combined antennal lobe/mushroom body model captures the features of the modified unique cue model. Additional features that are related more to the behavioral side, such as competition for attention or reduction in salience if elements occur in a compound stimulus, could be included in the model if one assumes some form of limitation in reinforcement per trial. Again one would have to keep in mind that reinforcement is represented both at the level of elemental processing (the antennal lobe) and compound stimulus processing (mushroom body) (Hammer, 1993, 1997). The consequence will be that elemental and configural tasks have different dependencies on such restrictions, and in the course of learning the balance between their contributions in controlling behavior may change.

VI. Conclusion

Formal models of behavioral routines are usually neither motivated by nor aimed at the neural mechanisms that cause these behaviors. The reason for this lies in the complexity of neural structures and mechanisms, and in the fact that formal models capturing essential properties of behavior are not specified a priori to address neural functions. The lower complexity of the insect brain offers the opportunity to build a bridge between such formal models and their potential implementation in the brain. We study Pavlovian olfactory learning in the honeybee under the strict control of conditioning experiments in order to infer the mechanisms by which odor compound stimuli are encoded by the nervous system, and ask whether the configuration of odor processing found can be related to brain mechanisms. Such an attempt is facilitated by the possibility of recording spatially and temporally resolved brain activity in those neural nets that process and learn the odors in the honeybee.

Our conditioning experiments are consistent in indicating that odor compound stimuli are treated in the bee brain according to the modified unique cue theory. According to this theory a compound stimulus (in our case a mixture of odors) is represented as the sum of the individual neural representations of the components plus a specific neural event, proper to the simultaneous occurrence of the compound stimulus components. Neurobiological studies of olfactory coding in the brain are in accordance with this theory. Mixture stimuli are not merely represented as the sum of individual neural representations of the elemental stimuli, but instead include specific odor suppression phenomena, proper to the joint occurrence of the mixture stimulus components. With distinct neural representations for the components and the unique cue at hand, the honeybee brain could extract the necessary information for solving elemental and nonelemental (e.g., configural) olfactory discriminations in different parts of its olfactory pathway, the antennal lobe and mushroom body, respectively.

So far, combined efforts between psychological and neurobiological studies have led to a model, which presents a possible implementation of the processes involved in elemental and configural learning. This model makes specific predictions that can be tested in further experiments. For example, if elemental learning is indeed the function of the antennal lobes, while nonelemental (e.g., configural) learning requires the extraction and comparison of the neural representations of components and unique cues and occurs upstream of the antennal lobes, at the level of the mushroom bodies, it should be possible to selectively interfere with elemental and nonelemental processing. This research strategy has already provided some hints supporting the model (e.g., Malun et al., 2002). Even more attractive
is the possibility of changing the nature of the olfactory representations at
the antennal lobe level to facilitate or block the resolution of a given
olfactory discrimination in elemental or nonelemental terms. For instance,
it is conceivable that a given mixture stimulus results in a more or less
pronounced suppression phenomenon (glomerular inhibition) that can act
as a unique cue, thus making it possible to solve a negative patterning
problem. In such circumstances, it would be theoretically possible to accen-
tuate or suppress inhibition during mixture stimulus presentation by means
of pharmacological experiments and thus to determine the impact of such
interference in the choice of elemental or nonelemental discrimination
strategies. Functional imaging studies in the course of elemental and con-
figural learning tasks will also allow us to ask how the different memory
traces are combined to lead to coherent behavior in retrieval situations and
when memory is updated during new learning.

We believe that the present article exemplifies a research strategy that
proves to be rewarding and mutually enriching, one in which the power of
different domains, experimental psychology and neurobiology, is exploited
in working toward a common aim: the understanding of compound stimu-
lus processing and learning by the nervous system. Such combined research
is possible because the choice of an appropriate model system, the honey-
bee, allows us to address questions in both domains experimentally. With
the results of the experiments at hand, future research must deepen the
modeling approach in order to obtain a more precise physiological model of
the olfactory circuit capable of accounting for both the behavioral perfor-
mannces measured in this project and other unrelated behavioral find-
ings. There are fair chances of attaining this goal using the honeybee, a
model in which different domains converge and enrich each other in
a multidisciplinary and productive way.

VII. SUMMARY

We address the question of whether the nervous system treats and learns
a sensory compound stimulus as the simple sum of its components, or as an
entity different from them by using olfactory discrimination and learning in
honeybees. To study elemental and nonelemental forms of learning in
honeybees, we use olfactory classic conditioning of the proboscis exten-
sion reflex. In our paradigms, bees had to learn to discriminate mixture stimu-
li from individual components. We find that a modified unique cue
model best describes the results, indicating that both the elements of a
compound stimulus as well as a unique cue that is specific to the compound
stimulus are processed and learned in parallel. In a next step, we review

findings using optophysiological recordings from the antennal lobe of the
bee. Special emphasis is given to the question of how the combinatorial
activation pattern of glomeruli induced by an olfactory mixture stimulus
corresponds to the simple sum of the activation patterns elicited by the
single components of the mixture stimulus. We show that the local inhibi-
tory network of the antennal lobe leads to nonlinear summation and
suppression effects such that the neural representation of a mixture stimu-
lus includes the representations of the components but also odor-specific
inhibitory phenomena, which may correspond to the unique cue. Further-
more, it is noted that olfactory memory resides in both the antennal lobe
and the mushroom bodies, the second-order neuropil. We compile these
results in a model of olfactory processing and learning that assumes associ-
ative learning to be implemented both in the antennal lobe and the
mushroom body. The model predicts that elemental forms of learning
dominate associative processes in the antennal lobe and nonelemental
forms of learning in the mushroom bodies. Preliminary data support these
predictions.

The aim of this article is to demonstrate the applicability of physiological
interpretations of behavioral categories for a less complex nervous system.
In the case of the honeybee, our original question on compound stimulus
learning and perception can be studied at both psychological and neural
levels in order to decide between different models of compound stimulus
processing.

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Begging, Stealing, and Offering: Food Transfer in Nonhuman Primates

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I. Introduction

The idea that eating and sharing meat played an important role in human evolution (Isaac, 1978) has led to considerable interest in reports of hunting and meat sharing in chimpanzees (Stanford, 1999). A detailed understanding of food-sharing behavior in chimpanzees and other nonhuman primates could arguably provide insights into the evolutionary history of food sharing in human beings. Although the role of meat eating and meat sharing in human evolution remains a highly debated issue (Stanford and Bunn, 2001), the pervasiveness of food transfer within contemporary human societies is beyond doubt (Gurven, 2004). What benefits might individuals obtain from allowing others to gain access to their food? Several evolutionary explanations have been suggested for the benefits of transferring food to other individuals, including kin selection, reciprocal altruism, and costly signaling. While the literature on food transfer in human beings has been compiled and evaluated recently (Gurven, 2004), the latest review of the subject in nonhuman primates was published more than a decade ago (Feistner and McGrew, 1989). The aim of this review is to bring together theoretical and empirical work on food transfer in nonhuman primates (hereafter referred to as “primates”). While food transfer has also been found to occur in a broad range of species, including insects, birds, cetaceans, bats, and other mammals (reviewed by Stevens and Gilby, 2004), such behavior has been particularly well studied in primates.