J. comp. Physiol. 121, 65–77 (1977)

Journal of Comparative Physiology · A

Visual Interneurons in the Median Protocerebrum of the Bee

J. Erber and R. Menzel* **

Institut für Tierphysiologie, Arbeitsgruppe Neurobiologie, Freie Universität Berlin, D-1000 Berlin 41

Received May 25, 1977

Summary. Visual interneurons in the median protocerebrum were electrophysiologically analysed. Over half of the units responded to more than one modality (light, scent, sugar water). As the intensity dependencies for these interneurons are rather complicated, their visual properties were characterized by measuring response/intensity functions (R/I-curves). No significant response differences were found for the different recording locations in the mushroom body region. The only apparent difference was that the interneurons' spontaneous discharge frequencies differed with recording site.

The visual interneurons revealed different classes of R/I-dependencies:

1. R/I curves with positive slope and a wide response range;
2. R/I curves with intensity specific response bands (I-bands);
3. R/I curves with inhibition;
4. R/I curves with little intensity dependence;
5. R/I curves with colour specific response bands.

The spectral sensitivities of most units were broad. In all but one case narrow banded spectral sensitivities had a UV maximum. In many units the spectral sensitivities for the three temporal components of the response (on, sustained and off) are different. The integration of these neurons in the process of colour coding is discussed.

Introduction

The capacity of the bee to discriminate colours has been intensively studied by psychophysical methods since von Frisch (1914) published his classical training experiments (Daumer, 1956; Menzel, 1967; von Helversen, 1973). Electrophysiological measurements of the photoreceptors' spectral sensitivities demonstrated three major classes of colour receptor types with sensitivity maxima at 340 nm, 440 nm and 540 nm respectively (Autrum and von Zwehl, 1964; Menzel and Blakers, 1976). This finding is in good agreement with Daumer's (1956) conclusion that the honey bee has a trichromatic colour vision system

* Supported by the DFG, Grant No. Me 365/4

** We wish to thank Dr. J. Kien, Seewiesen, for helping us to prepare the English translation of this paper

consisting of UV, blue and green receptors. The neural processing underlying colour integration, however, is barely understood. Recordings from single neurons in the optic lobes (medulla and lobula) demonstrated broad band and narrow band neurons, the latter characterized by various degrees of colour opponency (Kien and Menzel, 1977a, b). In contrast to colour opponent neurons in vertebrates, colour antagonism in the bee optic lobes is not combined with spatial opponency.

The ability of bees to associate colours with food (Erber, 1975a, b) implies some kind of neural combination of the colour signal with other stimulus modalities such as sugar water taste. At what level in the brain such a coupling is established is unknown. We know from experiments with bees trained to odour that the mushroom bodies play an important role in the dynamic processes of memory formation (Menzel et al., 1973; Masuhr, 1976). It is an open question, however, whether the mushroom bodies are also involved in colour learning. Olfactory interneurons in the median protocerebrum were found by Suzuki and Tateda (1974), some of these neurons are modulated by the stimulation of the ocelli (Suzuki et al., 1976). Visual interneurons with inputs from the compound eyes have been recorded in the median protocerebrum of butterflies (Swihart, 1970, 1972; Schümperli, 1975), and these interneurons seem to be involved in colour coding processes. Multimodality, however, has not been studied.

Starting from this limited knowledge about the function of the mid-protocerebrum and especially of the mushroom bodies in bees, one may formulate two sets of questions, which we want to examine with electrophysiological methods: Firstly, are there visual interneurons and how do they differ in their response characteristics compared to neurons of the optic ganglia? Secondly, are such interneurons sensitive to more than one stimulus modality, and are there any adaptive changes after stimulation with more than one modality? This paper concentrates on the first set of questions; a following paper will examine the second question (Erber, in prep.).

The simplest way to test the neurons' chromatic properties is to stimulate them with spectral light of different intensities by using short light flashes. This seems also to be an appropriate way to study higher visual interneurons, since their integration properties and those of the preceding neurons are unknown. This experimental approach, however, has some limitations, which we have to keep in mind (see Discussion). Besides these stimuli we tested qualitatively the interneurons' sensitivities to odour and sugar water.

It is the goal of this paper to identify the parameters which determine the process of colour coding in the mushroom body area of the bee brain. Such an analysis is a first step in understanding the role of the median protocerebrum in the analysis of visual information.

Methods

Bees (*Apis mellifica carnica*, workers) were caught at the hive entrance and immobilized by cooling in the refrigerator. A single cooled bee was then mounted in a small metal tube by fixing its

head to the edge of the tube. The wings were cut off and the movement of the abdomen restricted by strips of sticky tape. The antennae, the proboscis, mandibles and legs were free to move. After a recovery period of about 40 min at room temperature the experiment started by mounting the metal tube on a ball joint in the middle of a perimeter device. The frontal head capsule was removed and the electrode was placed in the mid-protocerebrum immediately after removing the trachea covering the brain. The glass electrodes were filled with 3 M KCL and had resistances of between 90 and 150 MOhm in the preparation. The indifferent Ag-electrode was placed in the thorax.

Recordings were made in the area of the mushroom bodies (Fig. 1). The mushroom bodies are a dense neuropile formed by "intrinsic" fibres, whose pericarya are located in the calyx cup (Fig. 1, location 41) (Kenyon, 1898). The intrinsic fibres synapse with extrinsic fibres in the calyx wall (location 31), here the extrinsic fibres are presynaptic to the intrinsic fibres (Schürmann, 1971). The thin axons of the intrinsic fibres run parallel within the stalk (location 24) and branch at the basis of the α-lobe (the area surrounded by the locations 3, 4, 11, 13). Each intrinsic fibre sends a collateral both into the α-lobe and the β-lobe (location 13). These collaterals form synaptic contacts with extrinsic units in both lobes. Here the majority of intrinsic fibres are presynaptic to the extrinsic fibres (Schürmann, 1974).

The positioning of the electrode was facilitated by illumination of the brain directly from above. The α-lobes, the fibres surrounding the α-lobes and the median calyx wall are clearly visible under such illumination. The locations given in Figure 1 are defined relative to these landmarks. The recording depth was not measured.

The results are based on about 400 single unit recordings, 34 units were tested for their responses to monochromatic light flashes. All units gave action potentials between 5 and 60 mV. Except one unit (unit 117) the action potentials were positive. Recording stability was good, in some cases we were able to record up to one hour from one unit. The recordings were taped and filmed afterwards or evaluated by means of a frequency to voltage converter (Teledyne). In most figures neurons' activity is described by the relative spike frequency (fr). This is the ratio between spike frequency during or after the test stimulus and that shortly before stimulation.

Test stimuli were: Monochromatic light, odour and 30% sucrose solution delivered to the antennae or the proboscis. During stimulation with light flashes, the bee was kept in the dark, during olfactory and taste stimulation the room light was switched on. Monochromatic light was produced using a 900 W Xenon lamp, quartz neutral density filters and 5 interference filters (type DAL, Schott, Mainz) with transmission maxima at 363, 415, 472, 547 and 589 nm. In a few earlier experiments (Unit 19, Fig. 3; Unit 21, Fig. 5) we used NAL filters (Schott, Mainz) with broad transmission spectra and peaks at 424, 547 and 570 nm. In these experiments we produced UV light with an UG 11 filter (Schott, Mainz) with a transmission peak at 360 nm. The light flash was delivered through a flexible UV light guide which was mounted on a perimeter and subtended less than 2° at the bee's eye. We always stimulated the median part of the ipsilateral eye. The sequence of light intensities during stimulation was quasi statistic; to eliminate adaptation phenomena the sequnce of colours was varied unsystematically. Light intensity was measured as relative quantal flux using a calibrated thermopile. The odour was a mixture of thyme, lavender and rosemary. A piece of filter paper was soaked with this oily solution and placed in a glass tube through which air puffs were directed on to the antennae. The odour stimulus was not varied. In few cases, however, we tested if a puff of air without odour produced any response. Onset and duration of the odour stimulus was monitored by a small microphone.

Results

General Response Characteristics of the Units

Units responding to light flashes were found at all recording places (see Fig. 1). More than 60% of these units were bi- or multimodal, but a correlation of the type of multimodality with the various recording places could not be found. The spontaneous spike frequencies of the units range from less than 1 to 110 Hz. The lowest spontaneous frequencies were found at location 41, the highest

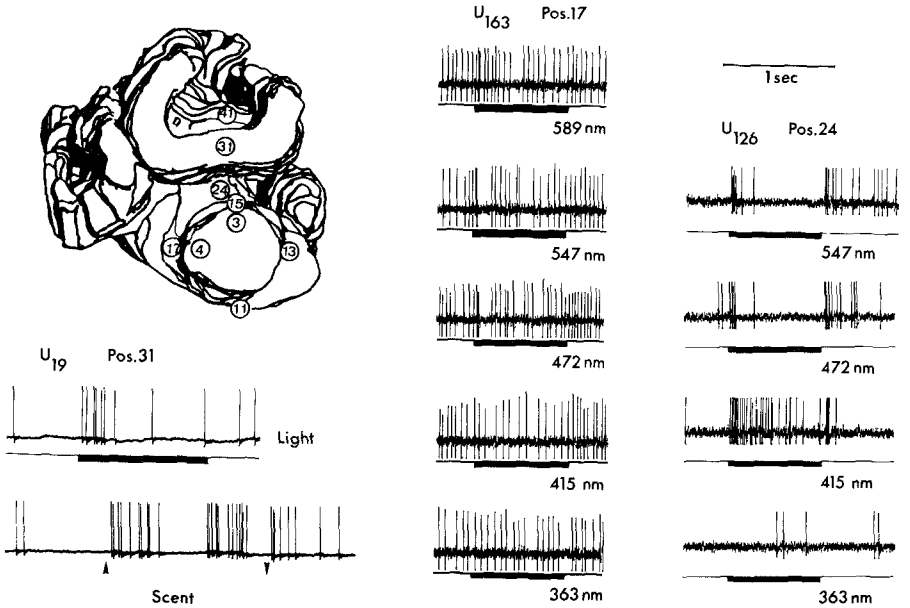

Fig. 1. Recording sites in the area of the mushroom bodies with three examples of interneuron recordings. The spatial structure of the right mushroom body was reconstructed from serial sections. Unit 19: stimulation with white light and scent. The wavelengths of the stimulating light for the other two units 163 and 126 are indicated. Pos. 17, 24 and 31 refers to the numbered recording sites

at location 13 (see Fig. 1). This difference in spontaneous discharge is the only significant effect correlated with the different recording sites.

The units' response to a light flash can be very different, ranging from excitation to inhibition. Examples are given in Figure 1. In this respect too, we found no correlation with the recording sites. The dynamic response range, i.e., the modulation of the spontaneous frequency caused by a stimulus, varies enormously. In general, neurons with low spontaneous discharge frequency display a larger response range (Fig. 1, unit 126) whereas units with a high spontaneous frequency show less modulation (Fig. 1, unit 163).

About 80% of the units recorded had broad spectral sensitivities with maxima around 363 nm and 547 nm. One unit was selectively sensitive to UV light in its sustained response, and selectively sensitive to orange light in its off response. All other narrow band neurons were sensitive only to UV. This is an important difference from the visual interneurons of the medulla and lobula (Kien and Menzel, 1977a, b). Furthermore, narrow band neurons are characterized by a generally smaller dynamic response range than the broad band neurons.

Neurons with Rising R/I-Functions

The statement that 80% of the neurons had broad spectral sensitivity functions is based upon the assumption, that the intensity dependence of the response

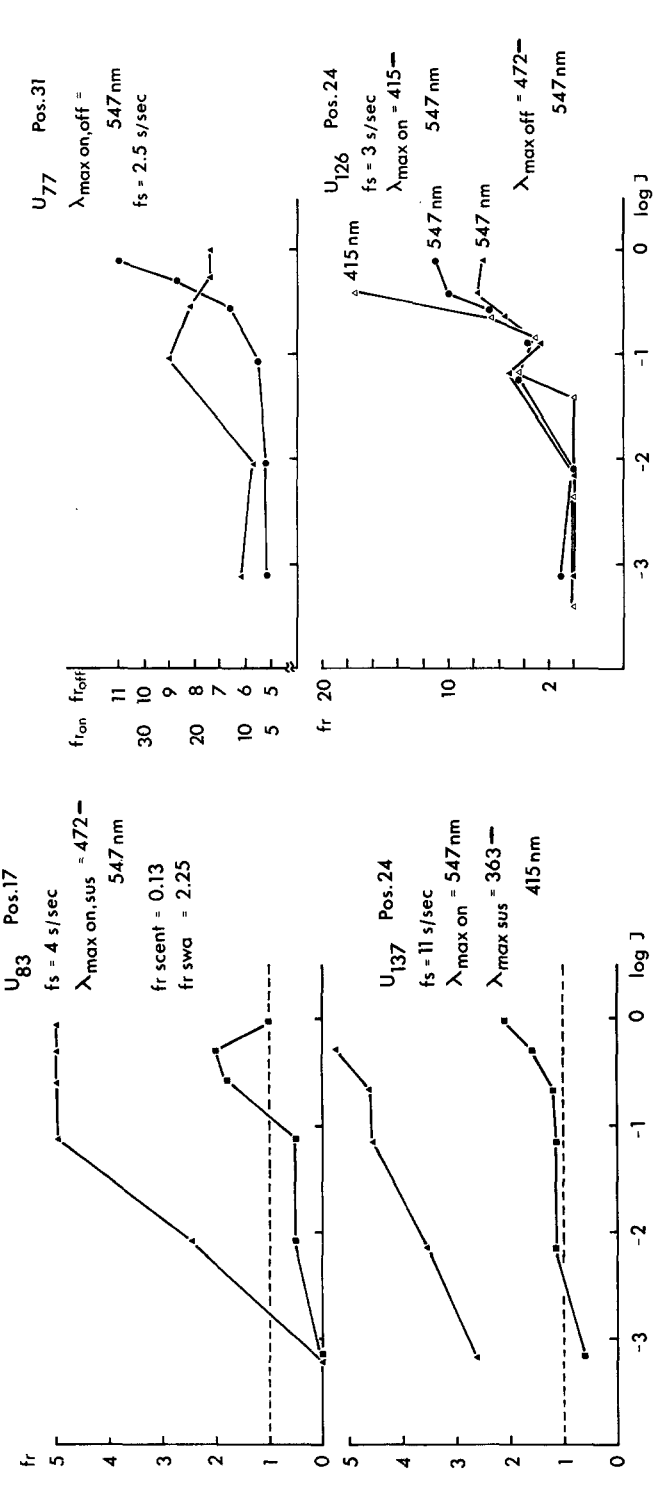

Fig. 2. *Four examples of neurons with rising R/I functions.* The wavelength of the stimulating light is always 547 nm; for unit 126 an additional R/I dependency for 415 nm is given. λ_{max} on, off, or sustained refers to the maxima of spectral sensitivity of the three temporal components of a units' response. fr scent and fr swa are the relative frequencies for stimulation with scent or sugar water to the antennae. ▲ = on-transient, ■ = sustained reaction, ● off-transient of the units evoked by light stimulation. Temporal duration of the three components: Unit 83: on = 0.1 s, sus = 1 s; Unit 137: on = 0.1 s, sus = 0,6 s; Unit 77: on = 0.2 s, off = 0.2 s; Unit 126: on = 0.3 s, off = 0.3 s. fs = spontaneous frequencies of the units', fr = relative frequencies; *abscissa*: relative logarithmic light intensities

(R/I function) for the various spectral lights can be used to calculate the spectral sensitivity of a unit. As the R/I functions of these higher order interneurons are frequently qualitatively different for different wavelengths, the determination of the spectral sensitivity relies critically on a complete and careful measurement of the R/I function for each wavelength and a comparison of equivalent response levels for the calculation of spectral sensitivity.

Four examples of broad band neurons with rising R/I functions are given in Figure 2. The intensity dependence of the different temporal response components (on, off, sustained) can be different both in threshold and in the slopes of the functions. Unit 83 for example has a simple rising R/I-dependence with an upper saturation for the on-response, but a sustained excitatory response only for a limited intensity band. This band occurs at a level where the on-response is already saturated. We shall discuss these "intensity band" responses below, because it is a characteristic feature found in many mid-protocerebrum neurons.

Unit 77 displays a comparable response behaviour for the on-component, whereas the off component has a rising intensity dependence. These two temporal transients were measurable even with the lowest intensities used in these experiments (-3 log units), indicating that the response of these interneurons covers a wide intensity range. Frequently the neurons differ in their threshold for the different temporal response components at the various wavelengths and, therefore, have different spectral sensitivity functions for on, sustained and off response (e.g., Fig. 2, unit 137). Such a neuron is sensitive throughout the whole spectrum with different sensitivity peaks for the three temporal response components.

Another remarkable property of these interneurons can only be analysed by measuring the R/I functions (Fig. 2, unit 126). Unit 126 (Fig. 2) shows only small differences of the response for the on-transient at low intensities with 415 nm and 547 nm. At higher intensities, however, there are significant differences for the R/I curves of the two colours. This effect could be measured repeatedly with this cell. In addition, the temporal response pattern differs for the different colour stimuli (Fig. 1).

These examples demonstrate that the determination of the spectral sensitivity of high visual interneurons is difficult because of the complex integrative processes within the optic ganglia. We believe that the knowledge of the R/I functions not only is a prerequisite for any determination of the spectral sensitivity, but also displays many features which help to understand aspects of visual coding mechanisms.

Neurons with Intensity Bands

Figure 3 gives two examples of interneurons which respond with excitation only to a limited intensity band. Such intensity bands can be broad (unit 19) or narrow (unit 37). They can be apparent in all temporal response components or only in one or two. These neurons demonstrate drastically that the R/I dependence has to be measured for as many test wavelengths as possible, other-

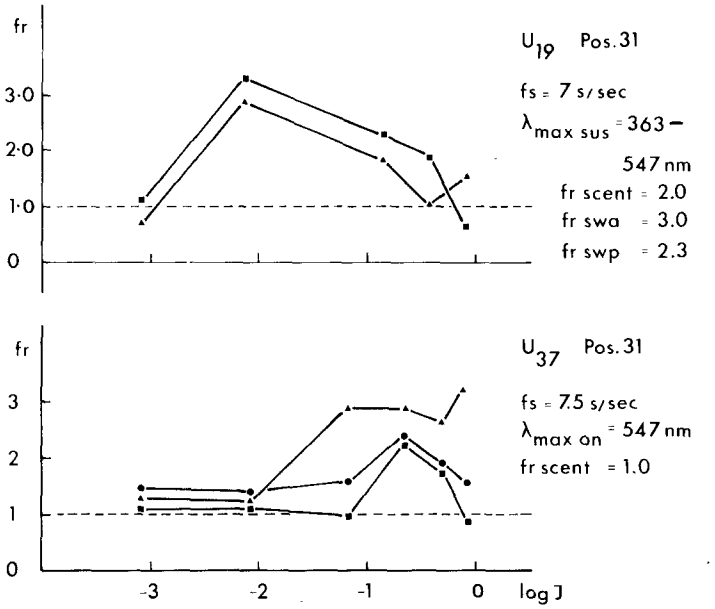

Fig. 3. Neurons with intensity bands. Unit 19: Stimulation with white light, the sensitivity maximum of the on-transient was not unequivocally determined. The relative frequencies for stimulation with scent (fr scent), sugar water to the antennae (fr swa) and to the proboscis (fr swp) are indicated. Unit 37: Stimulation with 547 nm, the sensitivity maximum of the on-transient was not unequivocally determined. The relative frequency for stimulation with scent is given (fr scent). ▲ = on-transient, ■ = sustained reaction, ● = off-transient of the units evoked by stimulation with light. Temporal duration of the three transients: Unit 19: on = 0.2 s, sus = 0.8 s; Unit 37: on = 0.1 s, sus = 1 s, off = 0.5 s. fs = spontaneous frequencies of the units, fr = relative frequencies; abscissa: relative logarithmic light intensities

wise the response cannot be assigned to the rising or the falling phase of the R/I function, and a determination of the spectral sensitivity would be impossible. Even a determination of the spectral sensitivity using a threshold response would be impossible.

Neurons with Inhibition

Decrease of spike frequency during and after light stimulation is a common response of visual interneurons in the mid-protocerebrum. We have not found any rule which temporal response component is more likely to be affected. There are examples where only one component is involved (e.g., unit 138, Fig. 4) or more than one (e.g. unit 85, Fig. 4). Interneuron 21 (Fig. 4) demonstrates nicely how complex the intensity dependence and the pattern of responses can be. The off-component gives increasing excitation with increasing intensity, the sustained response and the on-response decrease with increasing intensities. In addition, the spectral sensitivity differs for all 3 temporal components.

Unit 43 (Fig. 4) demonstrates several remarkable response features. Firstly, the degree of inhibition declines with increasing intensity of 415 nm light. Sec-

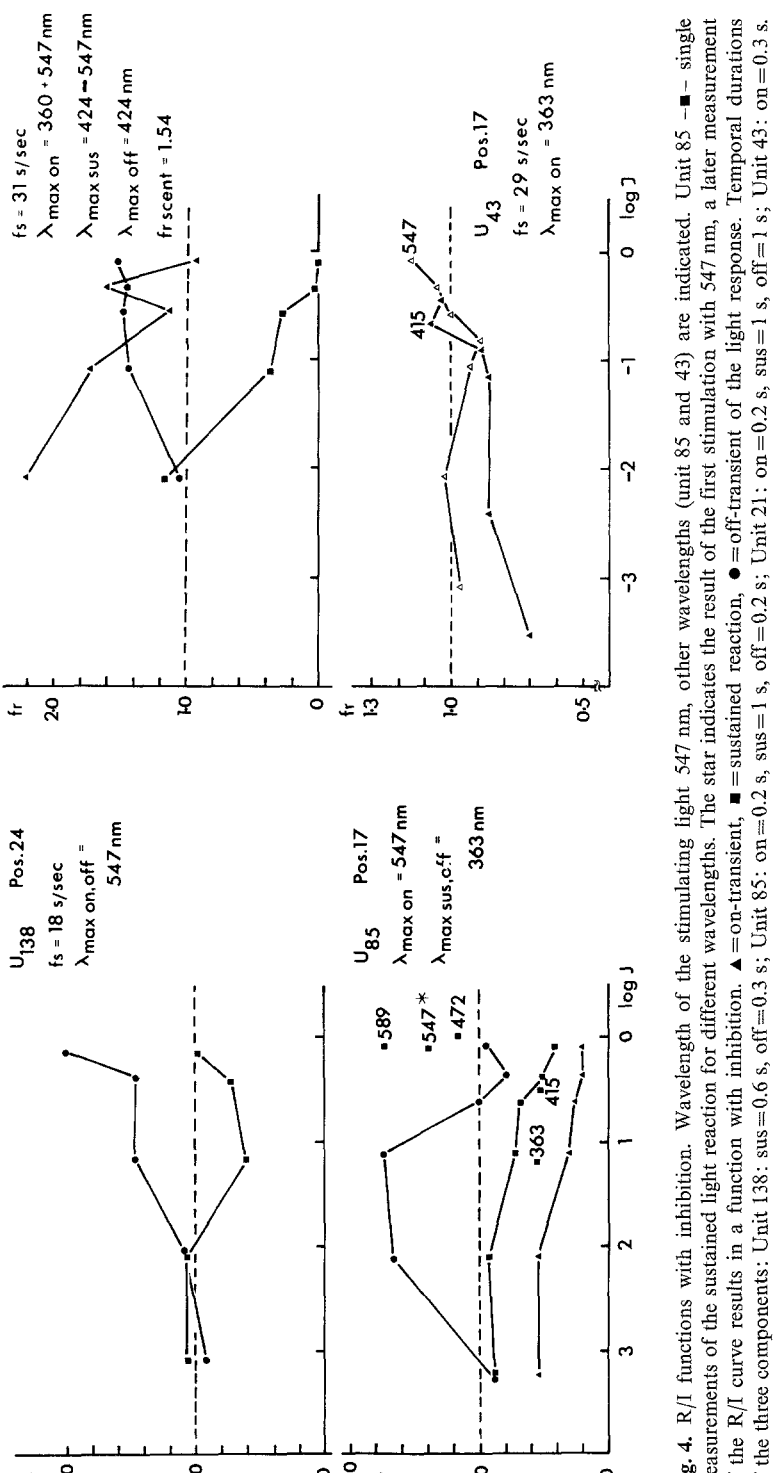

Fig. 4. R/I functions with inhibition. Wavelength of the stimulating light 547 nm, other wavelengths (unit 85 and 43) are indicated. Unit 85 –■– single measurements of the sustained light reaction for different wavelengths. The star indicates the result of the first stimulation with 547 nm, a later measurement of the R/I curve results in a function with inhibition. ▲ = on-transient, ■ = sustained reaction, ● = off-transient of the light response. Temporal durations of the three components: Unit 138: sus = 0.6 s, off = 0.3 s; Unit 85: on = 0.2 s, sus = 1 s, off = 0.2 s; Unit 21: on = 0.2 s, sus = 1 s, off = 1 s; Unit 43: on = 0.3 s. fs = spontaneous frequencies of the units, fr = relative frequencies; abscissa: relative logarithmic light intensities

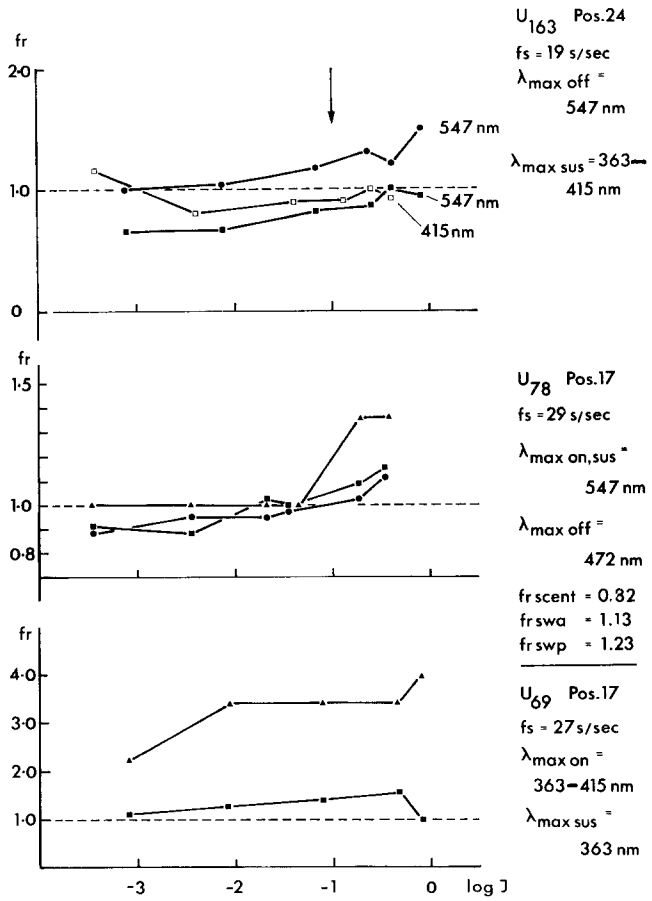

Fig. 5. Neurons with little intensity dependence. Stimulation always with 547 nm, for unit 163 the R/I curve for 415 nm is shown too. The arrow indicates the relative intensity used to calculate the spectral efficiency of the sustained reaction of unit 163. ▲ = on-transient, ■ = sustained, ● = off-transient of the light responses. Durations of the three temporal components: Unit 163: sus = 0.7 s, off = 0.3 s; Unit 78: on = 0.1 s, sus = 0.8 s, off = 0.5 s; Unit 69: on = 0.1 s, sus = 0.8 s. fs = spontaneous frequencies of the units, fr = relative frequencies; abscissa: relative logarithmic light intensities

ondly, the response range is very small over the 3 logs of intensity range, and thirdly, the response for 415 nm is different from that for 547 nm over more than 2 log intensity units. This last aspect will be discussed in more detail below. Unit 138 (Fig. 4) shows that the intensity band property can be combined with inhibition, too. Unit 85 shows another common response characteristic of protocerebrum neurons, their large variability to identical visual stimuli. The first stimulation with 547 nm caused an increase in spike frequency, a second identical stimulation during an intensity run resulted in an inhibition. Obviously, the response may change rapidly, but it is unknown whether this reflects an unreliability of the neuron response, or adaptive properties caused by inputs that were not controllable during the experiment.

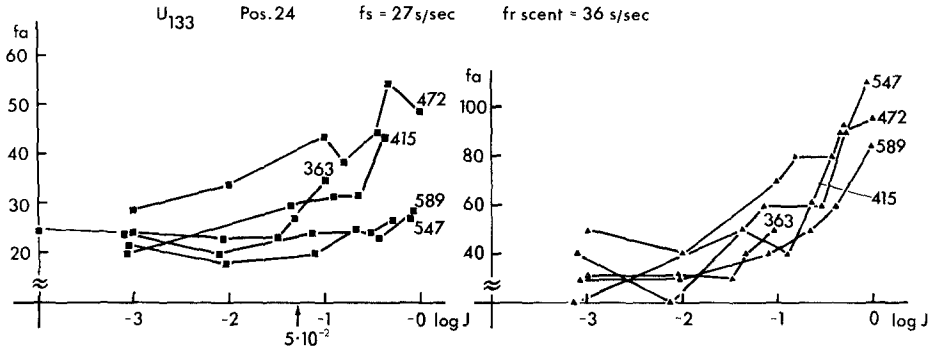

Fig. 6. Neuron with wavelength specific reaction bands. The wavelengths for the on (▲) and the sustained (■) components are indicated. The arrow indicates the relative intensity used for the calculation of spectral efficiency. Duration of the transients: On = 0.1 s, sus = 0.5 s, fs = spontaneous frequency, fa = absolute frequency in spikes/s (Hz); abscissa: relative logarithmic light intensities

Interneurons with Limited Response Range

Neurons with high spontaneous discharge rate usually have a limited dynamic response range. A subclass of these neurons are the units with very constant spike frequency. Such a neuron is shown in Figure 5 (unit 78). The spontaneous spike frequency in the dark was 29.4 ± 2.5 Hz for more than 40 min. The spike frequency rises in response to high intensity flashes for all 3 temporal response components, the slopes of the R/I curves are small. Comparable units were found in the butterfly brain (Schümperli, 1975), with the difference that their light response was restricted to the on-transient. All constant firing units in the bee brain were multimodal.

Units 69 and 163 (Fig. 5) are additional examples of units with limited response ranges. Unit 163 is remarkable in that the shallow intensity dependence results in separated R/I functions for the different wavelengths. This leads to another type of responses which may be involved in colour identification processes.

Neurons with Wavelength Specific Response Ranges

The extremely flat R/I function mentioned above could be a mechanism to code wavelength without or with reduced intensity dependence (compare unit 43, Fig. 4, unit 163, Fig. 5). This would be a quality which we would expect from true colour coding neurons. Figure 6 gives an additional example. The on-response produces similar R/I functions for different wavelengths. R/I functions based on the sustained response, however, differ significantly for different wavelengths. Long-wave light (547, 589 nm) produces R/I functions without intensity dependence over 3 log I units, shorter wavelength light produces rising R/I functions. The R/I function for 472 nm is separated from all other R/I

functions. The separation of the R/I functions does not allow the calculation of a spectral sensitivity function in the usual way. Alternatively one may calculate a spectral efficiency function, which shows a high sensitivity to blue-green light (472 nm), but even such a calculation may not reflect the true character of such a neuron. The follower neurons of such a cell would determine which of the parameters are enhanced or suppressed. A threshold in the range of 20 Hz could enhance the blue, to blue-green sensitivity. As naturally occurring intensity contrast is in the range of maximally two log I steps, such a follower neuron could discriminate between blue to blue-green and any other colour independent of intensity.

Discussion

Neurons in the median protocerebrum of the bee have complex response characteristics and differ in several aspects from those we have studied in the optic lobes. They can be uni-, bi- or multimodal to light, taste (sugar water on antennae or proboscis) and/or odour. They can have different spectral sensitivities for the different temporal response components (on, off, sustained). They can respond specifically for a limited intensity band and they can have fairly separate response levels for different wavelengths. However, we have not found any colour opponent neurons or narrow band neurons, which are so characteristic of the medullary and lobular region in the bee (Kien and Menzel, 1977b). We also have not found colour neurons as we know them from the vertebrate cortex (DeValois, 1973) which respond only to monochromatic light, not to white light and have no intensity dependence above threshold.

Such findings were unexpected on the basis of our limited knowledge of visual information processing in the bee brain. Judging from neuroanatomical findings (Strausfeld, 1975) the response characters of the interneurons in various areas within and around the mushroom bodies should differ considerably. Instead we have seen no functional differences in more than 400 single cell recordings, which were correlated with the recording site (see Fig. 1). Therefore, it does not seem justified to view the mushroom bodies exclusively as second order integration centers for olfactory inputs (Weiss, 1974; Strausfeld, 1975). Indeed, Suzuki and Tateda (1974) have found olfactory neurons in the median protocerebrum, but they did not test other modalities; their results, therefore, document only that olfactory inputs are integrated in this region; this is supported by our findings (see also Erber, in preparation). The new results of Suzuki et al. (1976) give evidence for bimodality in median protocerebrum interneurons. In this case it is the combination of inputs from the ocelli and from the antennae in interneurons of the median protocerebrum.

It is remarkable that the only significant difference between the different recording places refers to the spontaneous spike frequency, a result which has been reported by Suzuki and Tateda (1974) too. The significance of this result cannot be interpreted with our present knowledge. Neurons of the median protocerebrum are surprisingly unspecific in comparison to the complex mecha-

nisms of wavelength coding in the medulla and lobula. There seems to be no further specialization of visual interneurons behind the lobula. On the contrary, spectral sensitivities are obliterated, and additionally over half of the neurons are no longer specific for only one modality. Spatial parameters of the visual interneurons described here were not tested systematically. Qualitative observations indicate that the units found did not have complex receptive field structures, but were large field neurons with field sizes of more than 60 degrees.

We have found the R/I function to be the most sensitive parameter to describe the units' response characteristics. A functional classification based on the R/I functions reflects the complex properties of the units. The categories are: Neurons with intensity bands (Fig. 3). Neurons, which respond differently to different wavelengths at same intensities (Fig. 2, unit 126). Neurons with very small intensity dependence, which differ slightly for different wavelengths (Fig. 4, unit 43, Fig. 5, unit 163). Neurons which change their response characteristics rapidly (Fig. 4, unit 85). Neurons with a small intensity dependence, but different response levels for different wavelengths (Fig. 6).

Many neurons had different spectral sensitivities for the on, sustained and off response. One may argue that these differences result from our experimental procedure, mainly that we used high contrast flashes of monochromatic light to stimulate fairly dark adapted eyes. We cannot exclude this possibility, but as we also used flash intensities close to threshold and found the same differences we believe this feature to be a significant intrinsic property of the units. There are two possible interpretations for the different spectral sensitivities of the temporal response phases: Firstly, the nervous system could process the successive temporal components. This would lead to a temporarily specific transfer of spectral information. Secondly, the successively arriving spectral information could be averaged over time. In such a case most of the neurons described here would be broad band neurons without any colour specificity. If the first alternative is true one can model neurons filtering narrow banded wavelength specific responses, out of the temporal phases of a unit's response. Such a mechanism may play a role in successive colour contrast and release of wavelength specific responses, like proboscis extension (Daumer, 1958; for discussion see Menzel, in press). If the second alternative applies, visual interneurons in the protocerebrum are not involved in the colour integration processes but more in multimodality. Up to this date we have no experimental basis to discriminate between the two alternatives.

The question to be answered in this context is mainly related to the way how one sensory modality can modulate the response character of a neuron for another modality. Suzuki et al. (1976) have already reported most valuable observations on the interaction of ocellar and antennal input. Intensity band neurons and units with colour specific response levels are of major interest for an analysis of the interactions between colour coding and other stimulus inputs. Mainly the elements with different response bands for different colours could be involved in the process of colour identification. If the sometimes small differences in the response for different colours are detectable by follower interneurons, these elements would act as colour specific, nearly intensity independent neurons, and therefore would be "colour coding" elements.

References

Autrum, H., Zwehl, V.v.: Die spektrale Empfindlichkeit einzelner Sehzellen des Bienenauges. Z. vergl. Physiol. **48**, 357–384 (1964)

Daumer, K.: Reizmetrische Untersuchung des Farbensehens der Biene. Z. vergl. Physiol. **38**, 413–478 (1956)

DeValois, R.L.: Central mechanisms of colour vision. In: Handb. sens. physiol., Vol. VII/3A: Central processing of visual information (ed. R. Jung), pp. 209–254. Berlin-Heidelberg-New York: Springer 1973

Erber, J.: The dynamics of learning in the honey bee I. The time dependence of the choice reaction. J. comp. Physiol. **99**, 231–242 (1975)

Erber, J.: The dynamics of learning in the honey bee II. Principles of information processing. J. comp. Physiol. **99**, 243–255 (1975)

Frisch, K. von: Demonstration von Versuchen zum Nachweis des Farbensinnes angeblich total farbenblinder Tiere. Verh. dtsch. Zool. Ges., Freiburg (1914)

Helversen, O. von: Zur spektralen Unterschiedsempfindlichkeit der Honigbiene. J. comp. Physiol. **80**, 439–472 (1973)

Kenyon, F.C.: The brain of the bee. A preliminary contribution to the morphology of the nervous system of the Arthropoda. J. comp. Neurol. **6**, 133–210 (1898)

Kien, J., Menzel, R.: Chromatic properties of interneurons in the optic lobes of the bee. I. Broad band neurons. J. comp. Physiol. **113**, 17–34 (1977)

Kien, J., Menzel, R.: Chromatic properties of interneurons in the optic lobes of the bee. II. Narrow band and colour opponent neurons. J. comp. Physiol. **113**, 35–53 (1977)

Masuhr, Th.: Lokalisation und Funktion des Kurzzeitgedächtnisses der Honigbiene *Apis mellifica* L. Dissertation TH Darmstadt (1976)

Menzel, R.: Untersuchungen zum Erlernen von Spektralfarben durch die Honigbiene. Z. vergl. Physiol. **56**, 22–62 (1967)

Menzel, R.: Spectral sensitivity and colour vision in invertebrates. In: Handb. sens. physiol. VII/6 B (ed. H. Autrum). Berlin-Heidelberg-New York: Springer (in preparation)

Menzel, R., Blakers, M.: Functional organization of an insect ommatidium with fused rhabdom. Cytobiol. **11**, 279–298 (1976)

Menzel, R., Erber, J., Masuhr, Th.: Learning and memory in the honey bee. In: Experimental analysis of insect behaviour (ed. L. Burton-Brown). Berlin-Heidelberg-New York: Springer 1974

Schümperli, R.A.: Monocular and binocular visual fields of butterfly interneurons in response to white- and coloured light stimulation. J. comp. Physiol. **103**, 273–289 (1975)

Schürmann, F.W.: Synaptic contacts of association fibres in the brain of the bee. Brain Res. **26**, 169–176 (1971)

Schürmann, F.W.: Bemerkungen zur Funktion der Corpora pedunculata im Gehirn der Insekten aus morphologischer Sicht. Exp. Brain Res. **19**, 406–432 (1974)

Strausfeld, N.J.: Atlas of an insect brain. Berlin-Heidelberg-New York: Springer 1975

Suzuki, H., Tateda, H.: An electrophysiological study of olfactory interneurons in the brain of the honey bee. J. Insect Physiol. **20**, 2287–2299 (1974)

Suzuki, H., Tateda, H., Kuwabara, M.: Activities of antennal and ocellar interneurons in the protocerebrum of the honey bee. J. exp. Biol. **64**, 405–418 (1976)

Swihart, St.L.: The neural basis of colour vision in the butterfly, *Papilio troilus*. J. Insect Physiol. **16**, 1623–1636 (1970)

Swihart, St.L.: Modelling the butterfly visual pathway. J. Insect Physiol. **18**, 1915–1918 (1972)

Weiss, M.J.: Neuronal connections and the function of the corpora pedunculata in the brain of the American cockroach, *Periplaneta americana* L. J. Morph. **142**, 21–69 (1974)