

## Brain and Behavior

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### Calcium and calcium-binding proteins in the brain (Prof. Dr W. Zenker)

#### Parvalbumin, cytochrome oxidase and 2-deoxyglucose in the auditory and vocal motor system of adult zebra finches

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Auditory as well as vocal motor nuclei in telencephalon, diencephalon and mesencephalon showed high cytochrome oxidase (CO) activity combined with strong labeling with an antiserum against the  $\text{Ca}^{2+}$  binding protein Parvalbumin (PV) (Heizmann and Strehler 1979). In 2-deoxyglucose (2DG) experiments only the auditory nuclei were labeled. The correlation of 2DG and CO activities in the spontaneously active auditory system can be explained by energy consuming actual electrical activity (2DG) and by a large oxidative metabolic potential (CO). Since the vocal motor system was strongly CO positive but showed no 2DG labeling its actual electrical activity was low, however, it may be capable of a large increase, presumably during song production. In view of the prominent morphological plasticity in the vocal motor system even of adult birds (Gurney 1981, Rausch and Scheich 1982) the presence of the  $\text{Ca}^{2+}$ -binding PV in this system together with CO activity point to a role of  $\text{Ca}^{2+}$  for the modulation of activity and to a considerable energy demand of plastic changes in these nuclei during song learning.

### Distribution of calcium-binding proteins in the nervous system

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The anatomical distribution of cells immunoreactive towards antisera against the Vitamin-D-dependent calcium-binding protein (28k) (VDCaBP), Parvalbumin (PV) and S-100 are presented. In addition to a thorough analysis of their mapping in the adult rat brain, the ontogenesis and phylogenesis of these proteins are summarized. Particular emphasis is given to the comparison between the distribution of VDCaBP and PV with that of known neurotransmitters and peptides. Furthermore an attempt is made to assign VDCaBP and PV immunoreactive cells to neurocytologically defined types.

### Mitochondrial calcium accumulation in acute cerebral ischemia

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In order to determine the reversibility rate of neuronal lesions after ischemia, we studied the calcium accumulation in nerve cell mitochondria in a cat model, 30, 60 and 120 min after cerebral ischemia had been produced in the caudate nucleus

through a transorbital coagulation of lenticulostriated arteries. The opposite caudate nucleus of the same animal was used as a control. By means of electron microscopy and the oxalate pyroantimoniate technique, free calcium ions were located in the caudate nucleus of control animals and of those that had undergone ischemia. Cellular pathological findings included astrocytic swelling and degeneration of neurons, accompanied by a marked increase in the amount of calcium pyroantimoniate mitochondrial deposits. The content of intramitochondrial calcium deposits is related to ischemia duration as well as to the amount of cellular lesions.

### The role of calcium in the memory process of the brain

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The granule, CA1 and CA3 cells of the hippocampus have been much investigated during the last decade because there is superimposed on the standard feature of synaptic transmission a very prolonged potentiation lasting for weeks that is called long-term potentiation. Evidently long-term potentiation is a promising candidate in the construction of a model for memory. The thesis developed in my talk will be that the influx of calcium across the membrane of the granule and pyramidal cells plays the key role in the generation of long term potentiation. It is conjectured that the large increase of calcium in the granule and pyramidal cells results in its combination with the specific protein, calmodulin, to form a second messenger system which produces metabolic changes leading to an increase in receptors of the postsynaptic membrane for the transmitter glutamate.

### Vitamin-D-dependent calcium binding protein content is decreased in the cerebellum of diabetics

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The distribution of the 28,000 mol.wt vitamin-D-dependent calcium binding protein (CaBP) was studied in the cerebellar vermis of 14 diabetic (adult type diabetes) and 13 nondiabetic human subjects by immunohistochemistry using peroxidase-labelled anti IgG. In both groups, CaBP-immunoreactive material was found in perikarya, dendrites and axons of Purkinje cells, but when compared to controls, the positive dendrites and axons has had a significantly ( $p < 0.001$ ) reduced volume density in diabetics. This reduction was not due to an overall reduction in the number of Purkinje cell perikarya, dendrites or axons in diabetic cerebellar vermis. Alterations in the level of CaBP could interfere with the mechanisms normally involved in neuronal calcium-mediated events, and could contribute to the generation of the asymptomatic and symptomatic disturbances of diabetic neuropathy.

### Calcium-binding proteins in the brain. Structures and possible functions

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Calcium and a group of structurally homologous calcium-binding proteins play a pivotal role in the function of the nervous system and maintenance of long term neuronal viability. Calmodulin is a major  $\text{Ca}^{2+}$ -receptor protein possibly involved in the release of neurotransmitters and axoplasmic transport. In contrast, the function of the  $\text{Ca}^{2+}$ -binding S-100 proteins remains unknown. They are present in astrocytes but not in neurons or other glial cells. Parvalbumin, a specific  $\text{Ca}^{2+}$ -binding protein involved in the relaxation process of fast-twitch muscle fibres, has also been isolated from brain tissue and found to be present in a subpopulation of neurons in the central nervous system (for review see Heizmann, *Experientia* 40 (1984) 910). The possible involvement of this protein in  $\text{Ca}^{2+}$ -dependent processes such as regulation of intracellular  $\text{Ca}^{2+}$ -concentration, neurotransmitter release or axoplasmic transport is under present investigation.

### Calcium-binding proteins in hypothalamic cultures from mouse

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Neuronal cell cultures were derived from 16 d old embryonic mice and grown in serum-free medium. These cells are able to differentiate in vitro, e.g. they form synapses around day 9 (de Vitry et al., *EMBO J.* 2 (1983) 199). The appearance of various  $\text{Ca}^{2+}$ -binding proteins, e.g. parvalbumin, a neuronal marker, the S-100 proteins, glial proteins, calmodulin, and a vitamin D-dependent calcium-binding protein ( $M_r = 28\text{K}$ ) have been investigated in cultures at different developmental stages (3, 6, 9, 12 d in vitro) by means of immunohistochemical and biochemical methods.

### Localization of parvalbumin and the vitamin D-dependent calcium-binding protein ( $M_r = 28\text{K}$ ) in the cerebellum of normal and rachitic rats

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Two calcium-binding and structurally homologous proteins, parvalbumin and the vitamin D-dependent calcium-binding protein (CaBP,  $M_r = 28\text{K}$ ), are present in the central nervous system of the rat. Both proteins have been found in subpopulations of neurons but not in astro- and oligodendroglial cells. The cerebellum was found to be the brain area of the highest concentration of these proteins. CaBP immunoreactivity was only found in most (but not all) Purkinje cells whereas all Purkinje cells as well as certain percentage of stellate and basket cells were stained with the anti-parvalbumin serum. While a vitamin D-dependency of the synthesis of the CaBP in non-neuronal tissues is well known, the distribution and concentration of both proteins in the brain seemed to be independent of the vitamin D status. It is suggested that these proteins may regulate intracellular  $\text{Ca}^{2+}$ -concentrations within these neurons but an involvement in other  $\text{Ca}^{2+}$ -dependent processes can not be excluded.

### Ultrastructural localization of parvalbumin in the song system of zebra finches

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Antibodies against muscle parvalbumin (PV) were found to bind to systems in the brain of rats (Celio and Heizmann 1984) and of birds particularly to the nuclei of the vocal system (Braun et al. 1984). We investigated the distribution of this  $\text{Ca}^{2+}$  binding protein in neurons of the vocalmotor nucleus HVC in the forebrain of adult male birds using the indirect immunoperoxidase technique. The HRP reaction product was located in cell bodies, nuclei, dendrites, axons and in postsynaptic densities. PV was found in the amorphous material of the cytoplasm as well as on intracellular membranes with the cisternae of ER and Golgi apparatus spared. The observations suggest, that PV exists in two states: a soluble and a membrane bound form. PV localization in postsynaptic densities indicates a participation in  $\text{Ca}^{2+}$  effects at the synaptic junction. Postsynaptic  $\text{Ca}^{2+}$  currents and PV dependent  $\text{Ca}^{2+}$  control may be relevant for the known function of HVC in song learning.

### Organizing principles in neuroendocrine systems (Prof. Dr W. Lichtensteiger)

#### The ontogeny of the control of gonadotropin secretion in the male rat

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The importance of hypothalamic hormones for differentiation of the fetal pituitary primordia was studied in male rats. In vitro, it was shown that rat primordia explanted at 13 days of gestation (d) spontaneously differentiate when maintained in organ culture, with the appearance of functional gonadotrophs. However, when the primordia are explanted at 11 d, differentiation occurs only if GnRH is present in the culture medium for 1 day (Begeot et al., *Neuroendocrinology* 38 (1984) 217). In vivo, GnRH was detected in the earliest brain tissue examined (12 d). High affinity binding sites or receptors for GnRH were detected as early as 12 d in fetal pituitary primordia. Intracellular presence of GnRH in gonadotrophs, as seen by immunocytochemistry was first visible at 14 d. LH was first detectable in the fetal pituitary at 17 d. In conclusion, GnRH is present very early in fetal life and appears to be essential both for differentiation of the gonadotrophs and for induction of the first LH secretion.

#### The pars intermedia pituitary neuroendocrine system in vitro: electrophysiological and endocrinological studies

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Pro-opiomelanocortin (POMC) peptides are secreted simultaneously from one cell type in the pars intermedia lobe of the pituitary. Since dopamine is an inhibitory agent to POMC secretions and is localized in nerve terminals in the pars intermedia, a study was undertaken to elucidate the functional association between these nerve terminals and the secretion of one POMC peptide hormone, alpha-melanophore stimulating hormone (MSH). Explants, which contained the pituitary neu-

rointermediate lobe plus the medio-basal hypothalamus whose dopamine cell bodies send their projections to the pars intermedia, were taken from 21-day-old rats and maintained in a perfusion chamber for several hours. Stimulating electrodes were placed in the arcuate nucleus or median eminence while a recording electrode measured stimulus-evoked activity in the pars intermedia and the medium was assayed for MSH. Stimulation caused a release of dopamine and inhibited both activities.

### Searching a cellular basis for the effects of neurohypophysial hormones on memory

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Neurohypophysial hormones can affect the retention of passive avoidance behaviors in the rat. Based on these data, it has been said that they might affect 'memory'. Studies performed in our laboratory to assess the effects of neurohypophysial peptides in the hippocampus do not support this view, but rather suggest that oxytocin could act as a transmitter in this part of the mammalian brain. Extracellular recordings were obtained from spontaneously active neurones in hippocampal slices from adult rats. Oxytocin applied to the bath at concentrations of 1 nM or greater excited some cells. The effect was reversibly antagonized by a synthetic structural analogue known to block the peripheral effects of neurohypophysial hormones. The effect of oxytocin was mimicked by a selective oxytocic agonist and with less potency, by vasopressin and by various synthetic structural analogues. Their relative potencies correlated with their uterotonic activity, but not with either vasopressor or antidiuretic activities. It was concluded that some hippocampal neurones possess oxytocin receptors.

### Structural homology and functional diversity of pro-opiomelano-cortin-derived peptide hormones

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ACTH, LPH, the MSHs, endorphin and the newly discovered adrenal growth and mitogenic factors are derived from the same precursor, pro-opiomelanocortin. The identical molecular origin and the structural homology of these peptides require a complex regulatory system for the processing of the precursor and a highly selective recognition mechanism at the level of the target cells. In particular the latter plays a key role in the control of the wide range of different physiological actions of the opiomelanocortins. From structure-activity and photoaffinity labelling studies it appears that the receptors for these peptides on different cell types vary considerably and that even receptors on one type of cell in different species may require different topological elements of the hormone for stimulation.

### $\alpha$ -Melanotropin. Interaction between brain and peptide hormone in early ontogeny

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The role of steroid hormones in brain development is well documented; in contrast, we do not know whether peptide hormones are capable of influencing the organization of brain circuitry in mammals. We studied this question on the rat pituitary intermediate lobe which secretes  $\alpha$ -MSH and  $\beta$ -endorphin. The fetal gland possesses D2 receptors for dopamine (DA), an inhibitory effect of DA is demonstrable after birth, but DA innervation develops gradually and tonic inhibitory control as well as the feedback action of  $\alpha$ -MSH on the tu-

bero-hypophyseal DA neurons is established only at the end of the 1st postnatal week, after a peak in plasma MSH. I.v. injection of  $\alpha$ -MSH antiserum during the MSH peak (day 5 and 6) prevents the development of  $\alpha$ -MSH feedback. These observations indicate that the development of central control of  $\alpha$ -MSH secretion is influenced by this peptide hormone.

### Hypothalamic secretion of dopamine and its regulatory role on prolactin

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Dopamine (DA) secreted by the tuberoinfundibular dopaminergic (TIDA) neurons of the hypothalamus is known to exert a tonic inhibitory control on the secretion of prolactin (PRL). The secretory activity of the TIDA neurons, including biosynthesis of DA and release of the neurohormone into hypophysial portal blood, can be readily evaluated in the rat. An acute reduction in the secretory activity of the TIDA neurons has been found after intracerebroventricular administration of ng doses of morphine and it is associated with an increased secretion of PRL. The previously reported augmentation of the secretory activity of the TIDA neurons observed after PRL treatment in young rats (3–4 months old) is not detected in aged rats (20–24 months old). In old rats a sustained reduction in the hypothalamic secretion of DA is observed in spite of long-term hyperprolactinemia, with a marked decrease in the activity of tyrosine hydroxylase in the TIDA neurons characterized by alterations in the kinetic properties of the enzyme.

### 'Natural' sleep-inducing compounds (Prof. Dr A. Borbély)

#### Long-term treatment of hyposomnia with L-tryptophan

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The treatment of insomnia with L-Trp often leads to a worsening of sleep, while a chronic treatment with L-Trp improves sleep in patients who suffer from insomnia for more than two years. In a double-blind 3-months study, L-Trp (n = 7) but not placebo (n = 6) increases significantly duration of total and slow waves sleep (stages 3 and 4). Free plasma Trp in the placebo group ( $1.72 \pm 0.37$  ng/ml) correlates with total Trp ( $r = 0.51$ ,  $p < 0.01$ ). In the Trp group, free plasma ( $2.0 \pm 0.93$  ng/ml) showed a significant correlation with total plasma Trp ( $r = 0.93$ ;  $p < 0.001$ ). There is a tendency for a correlation between free Trp and the increased duration of sleep. These investigations demonstrate the clinical effect of Trp in chronic insomnia and the possible role of free Trp as an indicator for amelioration of sleep quality.

### Pharmacological effects of valerian compounds, with special reference to valepotriates. Central depressant or smooth muscle relaxant action?

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The early claim that valerian preparations have a calming effect in man has not been objectively demonstrated. In this

study, extracts as well as isolated and purified compounds such as valepotriates and essential oil compounds were investigated in animal test models for evaluating central depressant and/or anxiolytic activity. In contrast to reference drugs (barbiturates, benzodiazepines, meprobamate) the investigated compounds were found to be inactive in these screening procedures after various routes of administration even at relatively high doses. However, didrovaltrate (a valepotriate) and valeranone (an essential oil compound) showed a pronounced smooth muscle relaxant action on the gastrointestinal tract. These compounds were shown to be equipotent to papaverine both in gut preparations in vitro and on guinea-pig intestinal motility in vivo. It was concluded that didrovaltrate and valeranone are possibly of therapeutical significance for treatment of emotional tensions accompanied by spasms within the gastrointestinal tract. Valerian preparations may therefore produce a calming effect indirectly through a local spasmolytic action.

### Nutrition, neurotransmitter function and behavior (Dr D. V. Ashley)

#### Behavioral responses of rats on high- and low-protein diets, as a function of early versus normal weaning

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High (22%) and low (13%) protein, casein diets, the same as those consumed by dams during gestation and lactation, were supplied to their pups (F<sub>1</sub>) from either day 18 (early weaning) or day 22 (normal weaning). The effects of these diets and the weaning methods on the growth, body composition and behavioral responses of the weanlings, were investigated.

The high carbohydrate-energy availability in the diet, despite the low-protein level, a) contributed to a rapid initiation of adaptive metabolic changes in the early-weaned rat, and b) was adequate to ensure a decrease in gluconeogenesis and an increase in lipogenesis, thus accelerating the course of events seen when rats are normally-weaned on postnatal day 22. Early weaning on postnatal day 18, per se had no modifying influence on the behavioral responses brought about by the low-protein (13%) diet.

#### Cephalic insulin secretion and oral glucose tolerance in genetically obese (*fa/fa*) rats

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Cephalic phase insulin secretion was studied in freely-moving lean and genetically obese (*fa/fa*) rats indwelt with chronic cardiac catheters for blood sampling. The animals were trained to drink either 1 ml saccharin or 1–2 ml glucose within 60–90 sec. Glucose ingestion was also compared to an i.v. glucose load. Compared to lean, cephalic phase insulin secretion expressed in percent of basal values was decreased in obese rats during saccharin or glucose ingestion. Plasma glucose disappearance was markedly slower in obese than in lean rats after glucose ingestion, while it was identical when glucose was given i.v. As cephalic phase insulin secretion is necessary for normal glucose disappearance, these findings may partly explain the abnormal tolerance to ingested glucose in the obese rats and could be due to altered signals to and from the CNS.

#### Maternal deprivation: effects on neurotransmitter and polyamine metabolism in the cerebellum of 10-day-old rats

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It has been shown that maternal deprivation induces a decrease of ornithine decarboxylase activity in the brain of 10-day-old rat pups (Butler et al., *Science* 199 (1978) 445).

In this study, we attempted to further clarify and differentiate the effects of maternal deprivation on neurotransmitter and polyamine metabolism. We also tried to discriminate between the effects of a lack of mother-infant interaction and those due to feeding disturbance.

The results show that maternal deprivation provoked a marked effect on cerebellum tryptophan, opposite to that on putrescine and also influenced related neurotransmitters and metabolites, although to a smaller extent.

#### Hyperinsulinemia of genetically obese *fa/fa* rats in an early and vagally-mediated event

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Experimental hypothalamic obesity has been shown to be partly due to the occurrence of early hyperinsulinemia that is vagus nerve-mediated. The aim of the present studies was to determine whether such was the case for the genetic obesity of Zucker (*fa/fa*) rats. Normal and pre-obese rats were studied at 17 days of age, time at which they were indistinguishable from each other. Those which became subsequently obese were retrospectively designated 'pre-obese'. For the tests, arginine (600 mg/kg) was injected with or without atropine (5 mg/kg) and plasma insulin and glucagon levels were measured. Pre-obese animals hypersecreted insulin as well as glucagon in response to arginine. These abnormalities were restored to normal by the acute pretreatment with the cholinergic antagonist, atropine. It is concluded that arginine-induced insulin and glucagon oversecretion in pre-obese rats is cholinergically mediated. As insulin hypersecretion occurs early (17 days), it may be causative in overstimulating lipogenic pathways and contribute to obesity.

#### Pterins in medicine. Biochemical, neurological, and immunological significance (Prof. Dr H.-Ch. Curtius)

##### Biosynthesis of tetrahydrobiopterin in man

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A phosphate-eliminating enzyme (PEE) from human liver was purified ca 1500-fold. PEE catalyzed the conversion of dihydroneopterin triphosphate to tetrahydrobiopterin (BH<sub>4</sub>) and inorganic triphosphate in presence of human liver sepiapterin reductase (SR), Mg<sup>++</sup>, and NADPH, showed a mol.wt of ca 63 kD on Ultrogel ACA 44, and was stable at 80°C for 5 min. The mechanism and possible intermediates in BH<sub>4</sub> formation were studied using stable isotope and mass spectrometry. Two deuterium atoms were incorporated into 1' and 2' position of BH<sub>4</sub> from (4S-deutero) NADPH, and one hydrogen from the

solvent at position C-6. This indicates an intramolecular rearrangement and formation of 6-pyruvoyl 5,6,7,8-tetrahydropterin. SR transferred the pro-S hydrogen of NADPH during the reduction of sepiapterin to dihydrobiopterin, whereas dihydrofolate reductase transferred the pro-R hydrogen in the reduction of dihydrobiopterin to BH<sub>4</sub>. Another possible intermediate, 2'-oxo tetrahydrobiopterin, was formed from BH<sub>4</sub> ( $K_m = 30 \mu\text{M}$ ) by SR and NADP at pH 9.

### Atypical phenylketonuria with tetrahydrobiopterin deficiency

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Tetrahydrobiopterin (BH<sub>4</sub>) deficiency is observed in three rare variants of hyperphenylalaninemia caused by molecular defects of GTP cyclohydrolase I (GTPCH), 'dihydrobiopterin synthetase' (DHBS), or dihydropteridine reductase (DHPR). By screening for BH<sub>4</sub> deficiency in 495 newborns with hyperphenylalaninemia, eight patients with 'DHBS' deficiency were detected. In a total number of 704 (including 209 older, selected) patients, one case with GTPCH deficiency, 39 cases with 'DHBS' deficiency, and 17 cases with DHPR deficiency were detected. Enzyme activity assays were developed for GTPCH in liver biopsies and stimulated mononuclear blood cells (heterozygote test), and for 'DHBS' in liver biopsies: In five patients with 'DHBS' deficiency, a deficiency of the phosphate-eliminating enzyme was proven; sepiapterin reductase activity was present. Subvariants can be recorded by measurement of homovanillic acid, 5-hydroxyindole acetic acid, pterins, phenylalanine, and tyrosine in cerebrospinal fluid.

### Adaptive plasticity in the central nervous system (Prof. Dr W. Precht)

#### Acoustic imprinting in chicks: differential <sup>14</sup>C-deoxyglucose uptake in the brain correlates with behavior

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Young guinea chicks (*Numida meleagris*) were successfully imprinted with tone bursts in a Y-maze where they had to approach and discriminate the imprinting stimulus. Imprintability lasted about 3 days. Experiments with 2DG were carried out in successfully imprinted chicks, experienced but unsuccessful chicks and naive controls of different age ( $N = 76$ ). Distinct 2DG labeling was found in nuclei of the auditory pathway in all chicks due to the tone stimulation. In contrast, three particular areas of the forebrain (parts of hyperstriatum accessorium, and of medial and lateral neostriatum/hyperstriatum ventrale) were labeled mostly in brains of successfully imprinted older chicks (Maier and Scheich, Proc. natn. Acad. Sci. USA 80 (1983) 3860). Hence these areas were suggested to be responsible for processing (i.e. attention, recognition and interpretation) of acoustic imprinting stimuli once they became definitely significant to the chicks.

### The development of motor nerves and its regulation: a quantitative study of the oculomotor nerve (ON) of *Xenopus laevis*

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In order to assess the occurrence and role of motoneuron death during development, the number of axons on the ON was counted in ultrathin sections of normal tadpoles and froglets as well as in tadpoles reared in 0.4 g/l thiourate (blocking metamorphosis). Under normal conditions, the total number of axons declines significantly during metamorphosis and the 3 months that follow. No such reduction is observed in animals kept in thiourate even after 3 months. Tadpoles that develop slowly (due e.g. to crowding, modifications in temperature and nutrition) and as a consequence stay in premetamorphic stages for months, do not reduce their number of axons, either.

Hence, it seems that metamorphosis coincides with, and is necessary for, neuronal death – as reflected by axon number – to occur.

### Functional architecture of the vertebrate visual system (Dr R. Kretz)

#### Development of neuronal numerical density in the visual system of the marmoset monkey

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Neuronal counts were made at different ages in the visual cortex (area 17) and lateral geniculate nucleus (LGN) of the marmoset monkey (*Callithrix jacchus*) from blocks embedded in paraffin, cut at 10  $\mu\text{m}$  and stained with cresyl violet. Neurons were counted on the medial surface of area 17 along strips from the surface to the white matter. Similar strips were studied in the central part of the LGN. Drawings were used to determine the nuclear size, number and position relative to the pial surface or LGN laminae. We calculated the volume of the LGN and area 17 at each age from reconstructions of serial sections, and estimated the shrinkage due to histological procedures. The volumes of the LGN and area 17 increase to a maximum a few weeks postnatally. Neuronal numerical density in both LGN and cortex falls sharply in the first postnatal month. There is no evidence for a change in total number of neurons from birth to adulthood in the visual cortex, but the adult LGN contains about one-third less neurons than the LGN at 1 month postnatally.

### Area 17 callosal projections in the adult tree shrew (*Tupaia belangeri*)

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Using retrograde transport of horseradish peroxidase interhemispheric connections of area 17 were examined in the adult tree shrew. Injection sites along the vertical meridian (17-18 border) exhibit a strong contralateral projection with a preponderant representation of the central retinal area. This projection along the vertical meridian can be called homotopical. However, injection sites in the remaining binocular segment of area 17 reveal a dispersed projection. Thus, these projections are also heterotopical. In addition, the heterotopic

projection seems to be less dense than the homotopic one. Most of the labeled neurons were found in supragranular layers and could be classified as pyramidal cells. In summary, the callosal projections of area 17 in adult *Tupaia* are different from those in cat and monkey, where in the adult animal inter-hemispheric, striatal connections are confined to the vertical meridian along the 17–18 border.

### Development of dendrites in the lateral geniculate nucleus of monkey

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Postnatal modifications of the dendritic tree in the lateral geniculate nucleus of the monkey were studied quantitatively in rapid Golgi sections with the aid of a computer microscope. There is first an increase in the mean length of dendrites, more pronounced in magnocellular neurons, followed by a progressive decrease lasting until adulthood. However, only terminal dendritic segments of both parvocellular and magnocellular neurons are involved in these changes in length, while intermediate segments are much shorter and show a more or less constant length throughout life. The terminal dendritic segments of both parvocellular and magnocellular neurons show a clear tendency to be oriented along fibres crossing the nucleus, while the orientation of intermediate segments is more random with regard to the fibres. These results suggest a greater plasticity of the dendritic tree in its terminal dendritic segments during development.

### The hippocampus as a focus of neuropharmacological research

(PD Dr H.L. Haas, Dr H.R. Olpe)

#### The hippocampus as a site of action for antipsychotic activity of neuroleptics?

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In the hippocampus (HP), we suggested that dopamine (DA) might play a transmitter role. Recently, we demonstrated the existence of DA receptors labeled specifically and stereoselectively in vivo by (<sup>3</sup>H)spiperone (SPI). The effects of a large number of neuroleptics on SPI binding in HP correlated very well with those in striatum. However, the atypical neuroleptics (which do not produce extrapyramidal side effects in clinic), inhibited SPI binding at lower doses in HP than in striatum. About 75% of the SPI labeled receptors in HP resemble those which are responsible for the increase of DA turnover in striatum, but not those responsible for catalepsy. The preferential effect of atypical neuroleptics on the receptors in HP led us to speculate on a possible role of these receptors in the symptomatology of schizophrenia, as well as in the therapeutic effect of neuroleptics.

### Adenosine enhances afterhyperpolarization and accommodation in rat hippocampal pyramidal neurons in vitro

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Adenosine added to the perfusion fluid of rat hippocampal slices at 10  $\mu$ M enhanced long lasting afterhyperpolarizations

after single action potentials, bursts of action potentials or calcium spikes. Accommodation of firing during a depolarizing pulse was potentiated. An increase in calcium dependent potassium conductance is likely to mediate these effects. Adenosine at concentrations of 50  $\mu$ M induced a hyperpolarization accompanied by a reduction in input resistance. The hyperpolarization could be reversed at  $-85$  mV. In TTX and TTX-barium treated slices the amplitude of the slow spike was decreased. This may result from a shunting of inward current in the dendrites due to an adenosine induced increase in potassium conductance. It is suggested that adenosine reduces pre- and postsynaptic excitatory signals principally by enhancing one or more potassium conductances. This effect is a powerful means for modulation of neuronal excitability and synaptic efficacy and can explain the antiepileptic activity of adenosine.

### Experimental genetics: brain and behavior

(Dr P. Driscoll)

#### Regional dopamine (DA) and noradrenaline (NA) utilization in Roman high- and low-avoidance (RHA/Verh and RLA/Verh) rats

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Differences exist between the RHA/Verh and RLA/Verh rat lines in serotonin (5-HT) metabolism in several brain regions. Also, three different experiments have demonstrated a higher turnover rate of DA, measured by the disappearance rate of its metabolite 3,4-dihydroxyphenylacetic acid (DOPAC), in the striata of RHA/Verh rats following monoamine oxidase inhibition (1895 ng DOPAC/g/h vs RLA/Verh: 1310 ng DOPAC/g/h). We have studied DA and NA levels in different brain regions of adult male rats for up to 3 h after an injection of the tyrosine hydroxylase inhibitor  $\alpha$ -methyl-DL-p-tyrosine (250 mg/kg, i.p.). %-reductions in NA were similar for both lines in the cortex (22,26), hippocampus (21,17) and hypothalamus (33,32), as were those for DA in the hypothalamus (50,51). Data for striatal DA supported earlier findings (above), which also indicated that there may be differences in the DA turnover rate (ng DOPAC/g/h) between the left (L) and right (R) striata of RHA/Verh rats (L = 2013 and R = 1495 vs RLA/Verh: L = 1210 and R = 1221). This possibility is being investigated further, as well as other aspects of DA and 5-HT metabolism in these lines of rats.

#### Differential proneness to learned helplessness in Roman high- and low-avoidance rats

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Rats of the RHA/Verh and RLA/Verh strains were tested for learned helplessness, using a triadic design: escapable shock (step-up avoidance, which RHA and RLA acquire equally rapidly), yoked inescapable shock (RHA-RLA crossyoked), and no shock (each group n = 12 per strain). The single session was 4  $\times$  20 trials, with successive shock intensities of 0.2, 0.6, 1.0 and 1.2 mA. During the next 8 days, the rats were tested with nine configurations of the Hebb-Williams water maze. Average latency to escape was increased in inescapably shocked RHA, relative to their escapable- and no-shock controls, but was not affected in the inescapably shocked RLA.

The greatest difference was in a reversal learning problem on day 4, which was learned by all groups except the inescapably shocked RHA. These results indicate that RHA rats are more susceptible to learned helplessness than RLA rats.

### **Behavioral comparison between RHA/Verh and RLA/Verh rats during the light/dark cycle**

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We have previously reported (Gentsch et al., *Physiol. Behav.* 27 (1981) 183) that RHA/Verh rats, when compared to RLA/Verh rats, are less emotional, showing a higher locomotor activity but a lower defecation score in an open field test. Here, we determined several behavioral parameters immediately after having exposed the rats to a novel environment and after a 4 h and 24 h adaptation period. Four experiments were carried out, each starting at a different time point within the light/dark cycle. Again, RHA/Verh rats exceeded RLA/Verh rats in locomotor activity after 0 h and 24 h, but not after 4 h, of adaptation. Behavioral parameters partly showed clearcut day/night variations, but differences between the two psychogenetically selected rat lines did not seem to be influenced by the time of day.

### **Effect of housing on nonsocial forms of behavior and on plasma hormone levels in roman high- (RHA/Verh) and low-avoidance (RLA/Verh) rats**

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The effects of individual- and group-housing on the behavior of adult male RHA and RLA rats were determined by measuring a) step-down latencies from a 15 cm high platform (37 × 22 cm) and b) the number and duration of acts/5 min when on a 40 cm high large perforated platform (90 × 60 cm). Step-down latencies were strain dependent (RHA < RLA) and, for RHA rats, housing dependent (indiv < grouped). On the large platform RLA rats were less active, more immobile, and groomed more than RHA rats. Plasma hormone levels of triiodothyronine, thyroxine and androgens, determined 4 weeks later after a 1-min transport stress, yielded no housing or strain differences. Increased corticosterone levels were significantly greater in group-housed rats. These results demonstrate housing and strain differences in even simple forms of nonsocial behavior. They also confirm and extend previous endocrinological findings with these strains of rats (Gentsch et al., *Physiol. Behav.* 28 (1982) 259).

### **Effects of repetitive defeat on learned submission and analgesia in two inbred strains of mice**

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Mice of two inbred strains (C57BL/6, DBA/2) were exposed to a single, or repetitive daily defeats. From the first to the last defeat session, C57 mice showed a decrease of escape behavior and an increase in defensive upright postures, whereas few changes were evident in DBA mice. A pronounced defeat-induced analgesia was recorded after the first and last defeat session in DBA mice, but only after repetitive defeat experi-

ence in C57 mice. During a confrontation with a non-aggressive partner 24 h later, learned submissive postures increased in repetitively defeated C57 mice compared to animals with a single defeat experience. Repetitive defeat experience did not significantly influence the sum of learned behavior in DBA mice. However, the pattern of learned responses changed, i.e. a decrease of escape responses was paralleled by an increase of defensive upright postures. This effect was most pronounced in mice which reacted with a conditioned analgesia upon contact with a non-aggressive partner. The results are discussed in terms of the influence of analgesic mechanisms on learning processes.

### **Psychogenetic differences in agonistic behavior not altered by restriction to a corn diet**

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The Roman high-avoidance (RHA/Verh) and Roman low-avoidance (RLA/Verh) lines of rats have been selected and bred for superior and inferior shuttle box avoidance, respectively. In addition to replicating the previously documented (Driscoll et al., *Physiol. Behav.* 24 (1980) 793) failure of RLA/Verh rat pairs to exhibit shock-induced fighting (SIF) at a low shock level and only minimal SIF at a high shock level, compared to the pronounced SIF exhibited by RHA/Verh rat pairs at both shock levels, the present study has also demonstrated that RLA/Verh rats exhibit significantly less predatory aggression than RHA/Verh rats. Neither form of agonistic behavior was significantly enhanced by restriction to a corn diet for several weeks, with the resultant decrease in whole brain 5-HT and 5-HIAA levels (Driscoll, Martin and Dedek, *Neuroscience* 7, suppl. (1982) S59).

### **Thyroxine reduces shuttle-box learning by increasing the number of mossy fiber boutons in mice and rats**

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Two-way avoidance acquisition and performance are known to be highly correlated with the number of mossy fiber terminals upon the basal dendrites of the hippocampal pyramidal neurons (Schwegler and Lipp, *Behav. Brain Res.* 7 (1983) 1). By means of three different genetic approaches, we found a strong negative correlation between morphology and behavior. Early postnatal hyperthyroidism increases the number of these synapses. We thus treated well-performing RHA-rats and DBA mice with thyroxine.

Thyroxine-treated animals showed both a decreased acquisition and performance of the shuttle-box task, with rats showing a dose-dependence. The number of synapses was increased in both species compared to saline-treated controls, and was highly correlated with the shuttle-box scores.

### **Defeat-induced learned submission and escape in mice: effect of genotype and drugs**

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Defeat-induced unconditioned and conditioned behaviors of C57BL/6 and DBA/2 mice were assessed in a social learning paradigm. Upon bites, mice of the DBA strain reacted with

significantly more escape reactions while C57 mice showed more immobile, crouch, and defensive sideways and upright postures. Clear genotype-dependent patterns were also evident from the conditioned responses recorded 24 h after defeat. DBA mice showed more escape, and defensive sideways and upright postures, upon contact with a non-aggressive partner mouse; in contrast, C57 mice reacted with more immobility and crouching. With an increasing number of bites (10, 30, 50) the sum of learned responses increased in C57 mice while it decreased in mice of the DBA strain. This decrement was paralleled by an increase in the defeat-induced analgesic response measured on the hot plate. The effects of long-acting opiate antagonists on learned behavior were tested in these two strains of mice, which differ in their opioid peptide systems. In general, the results point to the importance of stress-induced release of endogenous opiates in the regulation of adaptive processes.

### **The sensory effectiveness of supernumerary mystacial vibrissae (SWs) in the mouse; a deoxyglucose (DG) study of the barrelfield**

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SWs, in mice selectively bred for their occurrence (H. Van der Loos et al., *Neurosci. Lett.*, suppl. 14, (1984) S384), have been the subject of various morphological studies: their follicles, as those of normal whiskers, are innervated, surrounded by muscle slings and represented in the somatosensory cortex by barrels. Here, the response of supernumerary barrels to stimulation of SWs was compared to that of normal barrels using DG-autoradiography. Prior to stimulation, in two adult animals bits of mu-metal had been glued onto 2 C'-whiskers on the left side, and in five other mice onto whiskers C1, C2, C3 and E1, while all other whiskers were clipped. 12 h later, the mice were restrained, injected with [ $^{14}$ C]DG and stimulated with magnetic field bursts (6.7/s, 90–200 Gauss). After 45 min the animals were sacrificed. Autoradiographic images were obtained from sections of both hemispheres, cut tangentially to the barrelfield. Stimulation of SWs yielded an increased DG-uptake equal to that obtained after stimulation of normal whiskers, thus strongly suggesting that the extra sensory organs were fully effective.

### **Organization and neurobiology of spatial behavior (Prof. Dr K. Bättig)**

#### **Effects of monoamine depleters on nicotine-induced hyperactivity in the rat**

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The acetylcholine agonist nicotine is widely consumed by humans in the form of tobacco. When administered to rats in comparable doses to those taken by humans, it produces an increase in spontaneous activity. Such behaviorally effective doses of nicotine have been shown to increase brain noradrenaline (NA) turnover, and to decrease brain serotonin (5-HT) turnover. We are investigating the hypothesis that these neurochemical changes are causally related to the behavioral hyperactivity. In separate experiments, 5-HT and NA synthesis were blocked by administration of pCPA and FLA-63 respectively, in saline- and nicotine-treated rats. Both pCPA and FLA-63 antagonized nicotine's behavioral effects. Control experiments

to establish the specificity of these effects are currently in progress.

#### **Maze patrolling by rats with and without food reward**

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The purpose of the study was a) to measure exploratory efficiency of rats in complex mazes, and b) to establish whether this behavior is altered by providing food reward in the maze. Two maze configurations – Dashiell and six-arm radial – were presented consecutively for 6 days each. One group of 15 female RHA/Verh rats received 45 mg Noyes pellets in six distinct maze locations, another group of 15 never encountered food in the maze. In a separate experiment, the patrolling behavior of food-rewarded rats in the six-arm maze after depletion of all food was analyzed. In both experiments, food reward reduced speed of movement at the food locations and tended to reduce the efficiency of exploration. These results support the hypotheses that maze patrolling by rats is exploratory, not food-seeking.

#### **The role of visual extramaze cues in guiding spatial maze behavior by rats**

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There is evidence from the literature that for rats visual extramaze cues (VEC) are of considerable importance for establishing a spatial cognitive concept allowing an efficient exploratory patrolling of an elevated radial maze. In the present experiment, an automated tunnel maze of variable geometry was used to study the role of VEC in rewarded patrolling by rats deprived to 85% b.wt. For this purpose, one group of rats (NC) was tested in a radial tunnel maze configuration with no VEC available and compared to an other group (C) tested in the same arrangement but having a transparent plexiglass top. The C group showed less motor activity, an increased efficiency of patrolling, and tended to more stereotyped choice sequence in comparison to the NC group.

#### **Effect of age on behavior of rats in tunnel mazes**

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Behavioral measures were obtained from 20 senescent (30 months), 20 mature adult (17 months), and 20 mature young (5 months) female Wistar rats, using a completely automated tunnel maze system of variable geometry and an optional inclusion of a small open field in the center. In comparison with the mature young control group, mature adult and senescent rats showed an age-correlated decrease of spontaneous locomotor activity, an increase of open field anxiety and a decrement in exploratory patrolling efficiency, the latter indicating a deficit in spatial cognitive concept formation. The results give evidence for the aging process to be a rather complex behavioral syndrome.

#### **Woodmice orientation on a hole board: importance of proximal and distal cues**

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Male adult Woodmice were trained to find one hole out of 18 on a hexagonal board (cross section 156 cm, wall height 40



cm). The holes consist of removable metal tubes fitting into circular openings in the wooden board; their bottoms are either plugged or connected by a flexible tube to the home cage of the tested mouse. The mice ( $n = 30$ ) were given nine trials over a 3-day-period; before each trial, the table was rotated ( $60^\circ$ ,  $120^\circ$  or  $180^\circ$ ) and the holes were cleaned, but the board remained unwashed. The orientation of each mouse toward the training hole was then quantified while it was left for 1 min on the board with no open hole. Mice trained toward a fixed position in space spent much time in this sector, disregarding the proximal board cues. On the other hand, mice trained to find a hole related to proximal board cues (mainly olfactory ones), but at an unpredictable position in space, did not show any preference for a particular position on the board.

### Aspects of exploratory behavior of hippocampal rats in radial and hexagonal tunnel mazes

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A lot of research has been carried out concerning the functional properties of the hippocampal formation (hc). Various qualities were brought in contact with this brain area, e.g. the hc was seen as a 'cognitive map', a 'comparator', a 'working memory', etc. (for a review see J.A. Gray, Clarendon Press, Oxford 1982). In the present study, the exploratory patrolling of the hc-damaged rats (anterio-dorsal hc including fornix fibre bundle) was analyzed in a complex tunnel maze system described earlier (Bättig, K., in Zbinden, G., et al. [eds], Application of behavioral pharmacology in toxicology, Raven Press, New York 1983). In two separate experiments, using a radial arm configuration and several hexagonal configurations, hc-lesioned rats were found to be deficient in their spatial cognitive performances and to show significant changes in terms of the frequencies of visits of distinct loci and the correspondent transition times.

### Circadian rhythms and sleep in vertebrates and invertebrates

(Dr I. Tobler)

#### The circadian clock of the eyes: a pacemaker for locomotor activity rhythms of invertebrates?

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The sensitivity of the eyes of many invertebrates, at least molluscs and arthropods can be endogenously controlled by circadian clocks. Those 'eye clocks' are bilaterally organized and based on multioscillators which are anatomically integrated in the visual pathway (molluscs: Jacklet, *Science* 164 (1969) 562; crayfish: rev. Larimer and Smith, *J. comp. Physiol.* 136 (1980) 313; insects: Fleissner, *J. comp. Physiol.* 149 (1982) 311; scorpions: Fleissner, *Naturwissenschaften* 70 (1983) 366). Clocks which are responsible for circadian rhythms of locomotor activity are supposed to lie in the same area within the optic lobes (insects: Page, *Science* 216 (1982) 73).

Simultaneous recordings of ERG and running activity from beetles (Köhler and Fleissner, in prep.) and scorpions (Fleissner and Fleissner, in: Barth (ed.), *Neurobiology of Arachnids*, Springer, New York, in press) and successive recordings of both parameters in molluscs (Lickey et al., *J. comp. Physiol.* 153 (1983) 133, support the hypothesis that either the rhythms of ERG and locomotion share the same cir-

Experientia 41 (1985), Birkhäuser Verlag, CH-4010 Basel/Switzerland

cadian oscillators or the locomotor rhythm is driven by the 'eye clock' as its pacemaker.

### Sleep-wakefulness rhythms in honeybees – neurophysiology and behavior

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Results obtained in our laboratory from neurophysiological and behavioral experiments on forager worker honeybees support the assumption that bees experience sleep-like states during the night. The sensitivity of visual neurones is lowered at night but can be temporarily restored by arousal stimuli. Bees studied both in an outdoor observation hive and singly in the laboratory can remain motionless for long periods at night and may also display decreased postural tonus. In the laboratory, at night, the head and antennae of motionless bees assume, in a definite sequence, one of two typical constellations. Neither is seen during the day. Each constellation has a specific arousal threshold and both thresholds are higher than arousal thresholds measured during day time rest periods. These head/antennae constellations are thus probably reliable indicators of the depth of sleep in honeybees.

### When do crickets 'sleep'?

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Calling song of *Teleogryllus commodus* occurred during the early evening and the night, usually being expressed in continuous sessions of up to several hours in length. Locomotor activity was mainly distributed throughout the silent periods appearing in bursts of usually less than 1 h duration. The hypothesis that crickets 'sleep' at intervals during the day time was corroborated by the following observations: Individual *T. commodus* kept singly under LD 12:12 were disturbed at various times of the illumination period (max. once per 1–2 days). The hiding reaction expected on 'opening the cage' or 'touching the insect' was often absent or only appeared after repeated stimulation. Occasionally the cricket responded with (slow) movements of the antennae. Such reduced reactions can be interpreted to be equivalent of 'sleep' to sleep-like behavior in crickets.

### Invertebrate neurobiology

(Prof. Dr R. Wehner)

#### The TCG wind-sensitive interneuron in the locust and its role in flight behavior

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Many descending interneurons mediate sensory control of the locust 'flight motor'. One of these, the TCG, is particularly accessible to extracellular recording in flight and therefore warrants intense study. The TCG receives input from wind-sensitive head-hair afferents in the brain and conveys this information to the thoracic ganglia. The cell is rhythmically active in flight since the head hairs can detect the aerodynamic turbulences produced by the wing movements. The phasic discharge of the TCG codes the flight attitude of the animal with respect to the wind stream and this information is fed directly

to both flight motoneurons and to flight interneurons. These interneurons are rhythmically active in flight in either the elevator or depressor phase, receive sensory input from other modalities and are presynaptic to flight motoneurons. It is hoped that general principles of sensory control of movement will emerge from intensive study of this neuron.

### Behavioral evidence for polarization vision in crickets

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A cricket, *Gryllus campestris*, is offered a polarized wide field stimulus ( $83^\circ$ ) centered on the zenith. The tethered animal walks on a styrofoam ball supported by an air stream. Rotational and translational movements of the cricket are relayed to the ball (open loop situation). By recording the motion of the ball the cricket's turning tendency can be measured. When the polarizer rotates slowly ( $1.8^\circ/\text{sec}$ ) the turning tendency changes periodically as a function of e-vector direction. This reaction cannot be induced when the polarizer is replaced by a radial black and white grating ( $\lambda = 90^\circ$ ). By occluding different parts of the compound eyes with paint it is demonstrated that the reaction to polarized light is mediated by the anatomically (Burghause, Zool. Jb. Physiol. 83, 1979) and physiologically (Labhart et al., J. Comp. Physiol. A 155, 1984) specialized dorsal rim area of the eye.

### Warm and cold receptors of two sensilla on the foreleg tarsi of *Amblyomma variegatum* (Acari: Ixodidae)

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A pair of antagonistic thermoreceptors, a cold cell and a warm cell, has been identified in two long, tapering, poreless setae located distally on the foreleg tarsi. The cold units respond to a rapid drop in temperature with a sudden rise in impulse frequency ( $16.1 \pm 10.4$  (imp/s)/ $^\circ\text{C}$ ). The warm receptors respond to a rapid rise in temperature with a sudden rise in impulse frequency ( $17.6 \pm 9.5$  (imp/s)/ $^\circ\text{C}$ ). The calculated resolving power is  $< 0.41^\circ\text{C}$  for the cold cell and  $< 0.52^\circ\text{C}$  for the warm unit.

### Action spectrum of the extra oxygen consumption induced by light flashes in the honeybee drone retina

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In the drone retina, there is a transient increase in  $\text{O}_2$  consumption ( $\text{QO}_2$ ) after a light flash that occurs before Na pumping. Thus, there exists a signal stimulating metabolism distinct from use of ATP by the Na pump (see Tsacopoulos et al., Nature 301 (1983) 604). It is not known whether the extra  $\text{QO}_2$  is linked to phototransduction, which is triggered by rhodopsin, or whether it depends on a second photopigment. We have measured (using  $\text{PO}_2$  microelectrodes) the action spectrum of the extra  $\text{QO}_2$  produced by weak flashes of colored light. This action spectrum does not fit the rhodopsin absorption spectrum from microspectrophotometry, or the previously measured action spectrum of electrical responses. We have thus measured the action spectrum of electrical responses under the same conditions as for the  $\text{PO}_2$  measurements. This spectrum fits closely the action spectrum of the extra  $\text{QO}_2$ . The

discrepancy with the rhodopsin spectrum is explained as due to light scattering and/or absorption by screening pigments in the retinal slices used in these experiments. We conclude that the extra  $\text{QO}_2$  is linked to rhodopsin phototransformation.

### The projections of the three spectral receptor types in the cricket compound eye

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The projections of the three spectral types of receptor cell in the eye of the cricket (*Gryllus campestris*) were studied by intracellular recording and staining with Lucifer Yellow. This eye is characterized by an anatomically (Burghause, Zool. Jb. Physiol. 83, 1979) and physiologically (Labhart et al., J. Comp. Physiol. A 155, 1984) specialized dorsal rim area (DRA) which is involved in polarization vision (Brunner and Labhart, this volume). It is composed of blue receptors only, whereas the adjacent dorsal area (DA) contains UV and green cells. In the lamina, processes of all three types of receptor are found, each type showing its own pattern of short arborizations and spines. In contrast to the green receptors, all UV and blue cells stained cross the first optic chiasma and terminate in the medulla. The present results indicate that the axons of the blue cells (DRA) terminate in a more distal layer of the medulla than those of the UV receptors (DA).

### Biophysics and physiology of an identified nonspiking local interneurone in the CNS of the crayfish

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A pair of identified nonspiking local interneurons (LDS) in the terminal abdominal ganglion of the crayfish is depolarized by headward water movement via hair afferents on the tail fan. Depolarizing PSPs can be evoked by electrical stimulation of the afferent nerves to both sides of the ganglion. The LDS neurone in turn inhibits contralateral ascending interneurons. Analysis using switching single electrode current clamp (SEC) shows that ipsilaterally evoked depolarizing PSPs represent EPSPs whilst contralaterally evoked depolarizing PSPs are depolarizing IPSPs. Thus at the single cell level a cellular mechanism mediates contrast enhancement via lateral inhibition. Simultaneous recording from both LDS neurones reveals that contralateral inhibition is not mediated recurrently by the contralateral LDS interneurone. The interactions of ipsilateral EPSPs and contralateral IPSPs are discussed in relation to the anatomy and electrotonic properties of the LDS neurone.

### Circadian rhythm of light sensitivity: nocturnal and diurnal ants

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Two species of *Camponotus* ants, one nocturnal (*C. ligniperda*, CL; Switzerland), the other diurnal (*C. detritus*, CD; Namib desert), are compared with respect to visual acuity, light sensitivity, and light/dark adaptation. As CD sometimes stays outside the nest during the night, a strictly diurnal ant (*Cataglyphis bicolor*, CB; Saharan desert) is included in the comparison. Even though all three species are of about the same body size, the eyes of the diurnal species CD and CB are larger ( $1 = 800 \mu\text{m}$ ), contain more ommatidia ( $n = 1300$ ), and exhibit

smaller entrance pupils (diameter of rhabdom,  $d_r = 2.5 \mu\text{m}$ ) than the eyes of the nocturnal species CL ( $1 = 560 \mu\text{m}$ ,  $n = 450$ ,  $d_r = 8 \mu\text{m}$ ). Circadian pupillary responses (change of shape of the crystalline cone) occur in both *Camponotus* species, but are completely lacking in CB. Structural details of the pupillary response were studied by EM techniques, and the circadian rhythm of light sensitivity was monitored by long-term ERG recordings.

### Interneuronal circuitry for exteroceptive flight control in the locust, *Locusta migratoria*

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Flying locusts detect course deviations with three sensory systems: the compound eye, the ocellar and the windhair systems. Processed sensory information about detected course deviations reaches thoracic flight control centers by way of numerous descending sensory interneurons, many of which are multimodal. Each of these interneurons carries information about very specific forms of spatial deviation. These interneurons make connections onto many thoracic interneurons. Many of these thoracic cells are phasically gated by the flight central rhythm generator. They are thus the site of sensorimotor integration. This interneuronal circuitry modulates the activity of specific flight motoneurons and so effects correctional steering responses.

### Gravity perception of the tropical bont tick, *Amblyomma variegatum* (Acari: Ixodidae)

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Metastrate ticks possess four different types of intracuticular sensilla on their legs as revealed by electron microscopy. In order to determine if one or several of these sensilla play a role in gravity perception, the tracks of normal and selectively sensillectomized ticks running towards an IR source on horizontal or inclined planes are analyzed. The results suggest that ticks actually perceive gravity by means of intracuticular leg sensilla.

### Electrophysiological identification of specific receptor neurons for o-nitrophenol and methylsalicylate in *Amblyomma variegatum* (Acari: Ixodidae)

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The aggregation-attachment pheromone produced by fed and sexually active males of the tropical bont tick *Amblyomma variegatum* consists of the volatile compounds o-nitrophenol, methyl salicylate and pelargonic acid. Their activity and function in the aggregation behavior of the unfed males and females have been studied by in vitro bioassays (Schöni et al., in press). Subsequent to the morphological and structural studies of the tarsal sensory system of this tick (Hess and Vlimant, *Revue suisse Zool.* 89 (1982) 713) the perception of the phenolic components was studied by single cell recordings from wall pore single-walled (wp-sw) sensilla. Specific receptor cells for ONP were identified in wp-sw/A sensilla, while MS specific neurons are located in wp-sw/B hairs.

### Identification and action of the components of the aggregation attachment pheromone of *Amblyomma variegatum* (Acari: Ixodidae)

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Combining a new in vitro bioassay with the analytical method capillary gas chromatography-mass spectrometry, the aggregation-attachment pheromone produced by fed males of the tropical bont tick, *Amblyomma variegatum* was shown to consist of o-nitrophenol (ONP), methyl salicylate (MS) and pelargonic acid (PS) in the approximate amounts of  $2/1/8 \times 10^{-6}\text{g/tick}$ . A synthetic pheromone blend composed of these three volatile compounds evoked an aggregation response in unfed males and females comparable to the response to a natural pheromone source. Of the individual components, only ONP induced a significant, although not complete aggregation response. MS and PS contribute to a complete pheromone activity, but induce no aggregation at all, when offered separately.

### Temporal resolution of honeybee vision measured using heterochromatic flicker

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Temporal resolution of freely flying bees was measured by training the bees to discriminate a steady light from a flickering light of the same mean intensity and spectral composition. Initial experiments (Srinivasan and Lehrer, *Physiol. Ent.* 9 (1984)) reveal that the bees perform poorly at all frequencies when the flicker is homochromatic, regardless of the color of the light (UV, blue or green), but well when the flicker is heterochromatic. Heterochromatic flicker experiments using various pairwise combinations of the colors UV, blue and green (corresponding to the three receptor types in the bee's retina) reveal the integration time of color vision in the honeybee, and provide information on the time constants of the color channels and of their interactions. These experiments also provide a way of comparing the bee-subjective brightnesses of the three primary colors.

### A new method for studying the host-seeking behavior of the tropical bont tick, *Amblyomma variegatum* (Acari: Ixodidae)

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The device consists of two plexiglass chambers ( $40 \times 45 \times 70 \text{ cm}$ ) connected by a plexiglass tunnel closed at both ends by mobile doors. A rail crossing the whole apparatus allows the operator to move the ticks from one chamber to the other. Temperature, relative humidity and concentration of  $\text{CO}_2$  and odors can be set separately for both chambers. The experimentalist, who is hidden behind a shield, can study the reaction of the ticks to changes of environmental conditions through several peep holes. This method revealed that adult males of *A. variegatum* react weakly to changes in temperature, relative humidity and physiological  $\text{CO}_2$  concentrations when offered separately, but become highly excited by combined changes of temperature and  $\text{CO}_2$  concentration.

### **Surgically and genetically generated ectopic appendages allow to study neuronal specificity in *Drosophila***

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Surgical transplantation of imaginal disks in prepupae, and a number of homoeotic mutants have been used to create ectopic sensory neurons in *D. melanogaster*. Tracing of the central connections of these neurons allows to analyze the factors underlying the pathfinding of sensory axons within the c.n.s. In general, the ectopic sensory axons studied (i.e. from supernumerary wings, halteres, legs and antennae on the abdomen, or from homoeotically transformed antennae or probosces) terminate in the center of a serially homologous appendage or in the center of their own identity, but not in other regions of the c.n.s. Consequently, projection centers of serially homologous appendages might possess certain biochemical properties in common, which are not shared by other parts of the c.n.s.

### **Response of a wall pore single-walled sensillum of the tick *Ixodes ricinus* (Acari: Ixodidae) to 2,6-dichlorophenol (2,6-DCP)**

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2,6-DCP is an attractant sex pheromone of some metastriate ticks. Neurons of olfactory wall pore single-walled sensilla respond to this compound (Haggart and Davis, J. med. Ent. 18 (1981) 187). *Ixodes ricinus* which is a prostriate tick does not react to 2,6-DCP in behavioral experiments (Graf, Acarologia 17 (1975) 436). We however identified 2,6-DCP sensitive neurons in wall pore single-walled sensilla of the dorsal face of the foreleg tarsi by single cell recordings. These sensory hairs are innervated by six neurons with unbranched dendrites. The log-dose/response curve of 2,6-DCP neurons is sigmoid as in insect chemoreceptors. The role of 2,6-DCP in the biology of *Ixodes ricinus* still remains enigmatic.

### **Flight steering responses to visual stimuli by *Locusta migratoria* (L.)**

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A flight balance measures the forces and torques produced by a flying locust in response to movements of an artificial horizon. In these preliminary results only responses to a simulated roll are presented. It has been possible to confirm that indirect measures (e.g. muscle activity) of previous authors correspond to real changes in torques. Both the compound eyes and the ocelli can mediate these torques. The role of accessory flight muscle (85, 114) in the response to simulated roll, and the relationship between torque and latency shift in selected muscle units have been studied.

### **The functional anatomy of ocellar interneurons in the ant, *Cataglyphis bicolor***

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Photoreceptor cells in the ocelli of the desert ant *Cataglyphis* show similar spectral and polarizational sensitivities as the UV-receptors of the compound eyes (Mote and Wehner, J. comp. Physiol. 137, 63, 1980). However, there is no parallel alignment of ocellar receptor rhabdoms, as would be expected

for the detection of polarized light. In addition, there is a high receptor cell to second-order neuron convergence of about 30 to 1; yet *Cataglyphis* ants are nonetheless able to use their ocelli as an e-vector compass when their compound eyes have been masked (Fent and Wehner, Science 228, 192, 1985). Orthograde fillings of receptor cells with various marker substances (Cobalt, HRP, Lucifer yellow) reveal the optical tracts, the posterior slope area and the thoracic ganglia as the three major target areas of ipsi- and contralateral ocellar innervation. Retrograde fillings from these neuropiles are being used to gain information on receptor-to-interneuron linkages.

### **Anatomy of developing photoreceptor axons in the honeybee**

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The development of short (svf) and long visual fibre (lvf) projections from the developing compound eye to the lamina and the medulla was studied by orthograde fillings with horseradish peroxidase and by Golgi impregnations. Outgrowth of photoreceptor axons takes place during the prepupal stage. lvf and svf have growth cones with long filopodia. Three types of svf can already be distinguished in the pupal lamina. Up to the early pharate adult stage, two types of lvf can be discerned. They show different growth cone morphology, and their endings are located in different strata of the medulla. In adult workerbees, lvf are arranged in pairs, and their endings are located in the same stratum of the medulla.

### **The bee-dance controversy revisited**

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Von Frisch's classical view that bees read information about the location of a food source from the waggle dances performed by successful foragers has recently been challenged (Gould, Science 189, 685, 1975). Here we show that bees really use the spatial information encoded in the direction and velocity of the waggle dances, fly to the location indicated by the dancing bee, but finally appear at the food source only when some additional requirements (presence of other bees, odor) are fulfilled. The experimental trick used in unravelling this problem was to provide successful foragers dancing on a horizontal comb with ambiguous directional information by presenting them with a beam of polarized light in the zenith. Individually marked bees which had followed the ambiguous recruitment dances arrived not only at the food source previously visited by the dancing bee, but also at the location that was erroneously indicated by it. Only after these two (empty) sources had been searched thoroughly but unsuccessfully did some of the bees appear at other locations.

### **Light-induced increase in O<sub>2</sub> consumption in the barnacle eye**

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Invertebrate photoreceptors respond to light with a depolarization. The restoration of the ionic gradient is done by the Na<sup>+</sup> pump which requires metabolic energy. In muscle, work is followed by an increase of the oxidative metabolism resulting

from increased [ADP] (Mahler, J. gen. Physiol. 71 (1978) 533). But in the bee retina, light causes an increase of  $O_2$  consumption ( $QO_2$ ) which precedes the control (Tsacopoulos et al., Nature 301 (1983) 604). We have chosen the lateral eye of the barnacle (*B. eburneus*) for a further study of this control, since illumination of the photoreceptors is followed by a prolonged ( $\tau = 40$  s) and probably substantial pumping of  $Na^+$ . Using  $O_2$ -sensitive microelectrodes we have recorded a transient drop of the  $PO_2$  at the surface of the eye after a flash of light. Although calculation of the absolute  $QO_2$  will require further tests to choose a model geometry, results so far show that the time course of  $\Delta QO_2$  is similar to that of  $Na^+$  pumping.

### Control of insect reproduction

(Prof. Dr P.S. Chen, PD Dr H. Briegel)

#### Nitrogen excretion after blood meal in *Aedes aegypti*

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Female mosquitoes ingest considerably more blood protein than is required for oogenesis. The absence of nitrogen storage leads to excretion of nitrogen in substantial amounts. Besides uric acid, almost half of the excess nitrogen is excreted as urea, ammonia, protein, amino acids and hematin.

The temporal pattern of the nitrogen catabolites is characterized by two peaks. The first one (4–28 h after blood meal) contains uric acid, urea and ammonia, indicating the simultaneous operation of uricotelic and ureotelic pathways. This reflects the actual excretion of nitrogen catabolites. The second peak (28–48 h) is rather called defecation because it is marked by the expulsion of proteinaceous nitrogen (digestive enzymes) plus hematin, the latter in stoichiometric proportions with the hemoglobin ingested.

#### Physiological polymorphism in the dynamics of female reproduction in the yellow fever mosquito *Aedes aegypti*

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Quantitative analysis of excretion during the whole period of blood digestion and oogenesis in *Aedes aegypti* revealed three phenotypes in most populations tested: 'early, late, and intermediate' as distinguished by the time of hematin defecation in relation to uric acid excretion. These phenotypes are composed of time segments covering about 6–8 h each. Among the 14 strains of different geographic origin and laboratory history tested, varying frequencies of the phenotypes have been recorded. Crossing experiments are reported as well as correlations between physiological processes and the activity of the neuroendocrine system, both controlled by these genotypes.

#### Blood meal concentration and fecundity in the malaria mosquito *Anopheles*

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Female *Anopheles* were analyzed for the size of the blood meals and fecundity by measuring total nitrogen and hemoglobin in the host blood, in the midgut and in the pooled urine after termination of feeding and comparing it with the increase of fresh weight and the number of mature eggs in these females. In all three species tested, the blood protein is concen-

trated by a factor of approximately 2 during the act of feeding. This is achieved by instant and conspicuous urination processes during blood engorgement; in general, the clear urine contains no measurable nitrogenous material, except in *A. stephensi* where part of the hemoglobin is lost in a diluted form, rendering urine of bright red color. – *A. albimanus* was found to refeed once or twice after the first blood meal. By utilizing the protein of these subsequent meals for oogenesis, initiated by the first meal, fecundity was tremendously increased. This is in contrast to the yellow fever mosquito *Aedes aegypti* and bears epidemiological consequences.

#### Trypsin isozymes isolated from the female mosquito *Aedes aegypti*

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Midgut homogenates of blood-fed females of *Aedes aegypti* were subjected to ion-exchange chromatography followed by affinity chromatography. This simple two-step procedure revealed five major isozyme bands of trypsin with mol.wts of 26.7, 28.5, 29.7, 31.0, and 32.0 kD on SDS-PAGE. This isozymic pattern is comparable to the one in the raw homogenates. But several isozymes were found to segregate into subforms when analyzed by isoelectric focussing. By using  $^3H$ -labelled DFP as a marker for trypsin, a high correlation is demonstrated between TAME-active fractions and their DFP-equivalent on native acrylamide gels. Interference with blood-borne coagulation factors which often are of tryptic nature could be denied in our preparations.

#### On origin and function of hormones in embryos of an ovoviviparous cockroach *Nauphoeta cinerea*

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We have observed stage-specific variations in the titres of 20-hydroxy-ecdysone and juvenile hormone during embryogenesis, which suggest that the former induces cuticle formation and that the latter modifies this action by inducing the formation of a larva-type cuticle (Imboden et al., Gen. comp. Endocr. 36 (1978) 628; Imboden and Lanzrein, J. Insect Physiol. 28 (1982) 37). Our data show that the juvenile hormone originates in the embryonic corpora allata, since in vitro experiments with these glands have shown that they synthesize and release methylfarnesoate (the unepoxydized precursor of juvenile hormone III) and juvenile hormone III in stage-specific quantities. These two substances are found in varying and often large quantities in embryos at stages between dorsal closure and hatching; since methylfarnesoate seems to be rare or absent in later developmental stages, its occurrence in large quantities appears to be embryo-specific. Precocene application affects embryonic development and this approach promises to help in elucidating the precise roles of juvenile hormone and methylfarnesoate in the embryo.

#### Regulation of secretion protein synthesis in male accessory glands of *Drosophila*

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The secretory proteins in *Drosophila* male accessory glands are essential for sperm transfer and sperm utilization. By 1- and

2-dimensional gel electrophoresis we found that the protein patterns are highly species-specific, and there is evidence indicating that the major protein components act as isolating factors in interspecific crosses. Stimulation of secretion protein synthesis in the accessory glands can be detected within minutes after copulation is terminated. Repeated copulations elicit a stronger response. In vitro experiments have been carried out to analyze the molecular basis of the stimulating effect. In a reticulocyte-lysate system with added total accessory gland RNA secretory proteins appear as translation products, but there is little or no de novo mRNA synthesis. By contrast, the synthesis of ribosomal proteins and ribosomal RNA increases upon copulation.

### Effects of ingested ecdysteroids on a female tick

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Ingestion of 22,25-dideoxy-ecdysone (DDE) at doses as low as 35 ng/ml blood induced supermolting and reduced the egg number in females of the tick *Ornithodoros moubata*. Other ecdysteroids like ecdysone, 20-OH-ecdysone, Ponasterone A or Makisterone A showed similar effects, but at levels about 500 times greater than levels of DDE. Thus, *O. moubata* seems well protected against classical ingested ecdysteroids which contain a 22-OH group. It is likely that the recently discovered esterification mechanism at 22-OH with fatty acids is responsible for hormone inactivation.

### Effects of juvenile hormones and injected ecdysteroids on a female tick

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Juvenile hormones or analogues induce egg maturation and oviposition in fed virgin females of the tick *Ornithodoros moubata*. In contrast, ingested or injected ecdysteroids inhibit vitellogenesis e.g. through the induction of egg resorption. Injection into the hemocoel is much more efficient than ingestion. Doses as low as 100 ng per female induce supermolting and egg resorption.

### Early development of a dipteran egg in the presence of cytoskeleton-affecting drugs

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Embryogenesis in the paedogenetically produced larval eggs of the cecidomyiid insect *Heteropeza pygmaea* can be obtained in vitro. Using this system, the effects of cytoskeleton-affecting drugs on specific embryonic movements were filmed. It was found that development from the syncytial blastoderm stage to early germ band may occur in the presence of the microtubule-inhibitor colchicine, although orcein lactic acid staining shows that the following mitoses are arrested in metaphase. In contrast, germ band formation is suppressed by the microfilament-inhibitor cytochalasin B. The data show that the formation of the germ band is dependent on the activity of microfilaments but not on the number of preceding mitoses. The results also indicate that the different cytoskeletal elements (microfilaments and microtubules) have their own 'zeitgebers' for development.

### An in vitro system to study the incorporation of vitellogenin into the oocytes of the ovoviparous cockroach, *Nauphoeta cinerea*

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In our system for measuring vitellogenin incorporation in vitro, single ovarioles are incubated in heat-treated cockroach hemolymph containing  $^{14}\text{C}$ -vitellogenin. After working up oocyte membranes and oocyte content separately the amount of vitellogenin incorporated is measured by liquid scintillation counting. Dilution of the  $^{14}\text{C}$ -vitellogenin by the vitellogenin present in the hemolymph used for incubation is determined by using rocket immunoelectrophoresis. Analysis of the oocyte content using PAGE combined with liquid scintillation counting indicates that the majority of radioactivity incorporated is identical to vitellogenin. Our data show that vitellogenin is incorporated specifically, since other  $^{14}\text{C}$ -labelled hemolymph proteins are hardly incorporated at all. Vitellogenin uptake is linear for 12 h and dependent on the oocyte maturation stage. Oocytes at the stage of most rapid growth incorporate approximately 10–15  $\mu\text{g}$  vitellogenin/8 h. The use of this in vitro system should now allow us to investigate the precise role of juvenile hormone in regulating vitellogenin uptake.

### Specific binding of vitellogenin to oocyte membranes of the ovoviparous cockroach, *Nauphoeta cinerea*

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In order to investigate the presence of vitellogenin binding sites on the oocyte membranes and to study the mechanism of vitellogenin incorporation and its control by juvenile hormone we have developed an in vitro binding assay. In this assay oocytes are drained of yolk and the cortices, consisting of the oocyte plasma membrane, the follicular epithelium and the basement lamella, are incubated in an artificial medium containing  $^{14}\text{C}$ -labelled vitellogenin.

Using this method we observed that  $^{14}\text{C}$ -vitellogenin was bound to oocyte membranes of vitellogenic females in a saturable manner. Binding was shown to be specific, since unlabelled vitellogenin and vitellin competed with labelled vitellogenin for binding, whereas other proteins of female cockroach hemolymph did not do so. Binding reached an equilibrium within 1 h of incubation at 4°C or 26°C. The quantity of specific binding was proportional to the amount of membrane protein present in the assay. Scatchard analysis revealed a  $K_D$  of approximately  $6 \times 10^{-7}$  M and a concentration of binding sites of approximately  $10^{-7}$  M/g membrane protein.

### Behavior

(Prof. Dr H. Kummer)

### Mathematical models of optimal foraging in non-patchy habitats

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The classical models of foraging strategies assume that the food is distributed in patches and that the animal divides its time between the two distinct behaviors of patch exploitation

and inter-patch travel. As pointed out by Krebs and McCleery (in Krebs and Davies, *Behavioural Ecology*, 2nd ed., Blackwell 1984), this assumption is hard to accept in some instances such as an antelope grazing in the savanna, where the distribution of food is continuous in space. We present here models of optimal foraging in habitats where the food is distributed in space with an arbitrary density distribution. Travel and feeding can no longer be sharply distinguished. The problem is treated mathematically with the classical methods of calculus of variations. The patch models appear as special cases of the distribution models.

### Use of natural hammers by the chimpanzees of the Tai forest, Ivory Coast

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The chimpanzees of the Tai forest use clubs and stones to crack different species of nuts by placing them on emergent roots or outcrop rocks as anvils. We analyzed the behavior for two of the nut species: *Coula edulis* and the very hard *Panda oleosa*. The chimpanzees clearly adapt their choice of materials to the hardness of the nuts: For cracking harder nuts, they use harder and heavier tools that are rare in the forest and transport them more often and from farther away (Boesch and Boesch, *Behaviour* 3/4 (1983) 265). The common cracking sequence is illustrated in the poster. The chimpanzees crack *Coula* nuts on the ground or directly in the tree, *Panda* nuts on the ground only. An important sex difference was observed for the last two techniques: Adult females perform them more often than adult males (Boesch and Boesch, *J. Hum. Evol.*, in press).

### The orientation of the golden hamster to its nest site: II. The role of path integration

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When golden hamsters hoard food under IR light they return to their nest site using idiothetic or self-generated information gathered during their preceding outward journey. If the animal moves itself from the nest exit to the food source, it integrates both the angular and the linear components of its displacement and thus performs precisely orientated homing trips. After a passive outward journey, its return itineraries suggest that it has integrated only the angular, but not the linear components of its passive displacement. Experiments at present in progress aim at determining the limitations of the hamster's capacity to assess a) angular and b) linear displacements; it is conjectured that during passive displacements the latter are evaluated through the stimulation of a) the semicircular canals and b) the otolith organs. Further investigations concern the criteria used by the animal for initiating the measurement of idiothetic information, which in normal conditions, starts to be integrated at the very beginning of a hoarding trip.

### On the relationship between moorhen and coot chicks and their nesting-area as seen in natural and altered circumstances

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The populations of the coot have strongly increased recently, that of the moorhen, however show rather a decreasing ten-

dency. We thought that the needs of the two sympatrically existing species unequally well agreed to the conditions of their habitats continually changing by human influence. This study aimed to understand the coot and moorhen chicks as to their needs concerning their nesting area, i.e. from the behavior of hand-reared chicks kept under identical conditions. Contrary to coot chicks, moorhen chicks almost exclusively frequent dense vegetation for feeding and resting purposes, as well as for protection; they react more sensitively to intrusion, which has a more sustained impact on them and they don't easily adapt to changing conditions. So we discern a need for a living area with little intrusion and dense vegetation in the moorhen chicks only. With regard to a similar situation concerning adult birds, we are led to expect a further negative development of moorhen populations.

### The whistles of the alpine marmot (*Marmota m. marmota*) – their structure and occurrence in the antipredator context

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The aim of this study is to describe the whistles of the alpine marmot given in front of different predators and the responses of conspecifics to them. Observations and recordings performed in 1979 and 1980 in the Bernese Alps led to the following results: Whistles differ in the number of consecutively uttered elements, in the interval between the elements and the duration of the elements. Three classes of whistles were discerned: Single element whistles, whistle series and whistle sequences. In front of aerial predators (e.g. golden eagle, *Aquila chrysaetos*) and attacking foxes (*Vulpes vulpes*), marmots used single element whistles. Against foxes and humans approaching in a distance whistle series were the rule. This indicates that the marmots' whistles differ according to the imminence of predation. Single element whistles were stronger responded to by conspecifics than whistle series, thus indicating that they are understood as more serious alarm signals.

### Influence of man on social behavior of farm cats

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Different social patterns have been stated on five farms. The cats of two farms frequently slept together, licked each other, and formed a close amicable association. The cats of two other farms avoided interactions outside the breeding and mating season, and else seemed to associate mainly because of their common food source. The cats of the fifth farm either had ties to only certain colony members or lived solitary at all. During hunting and exploring all cats usually were nonsocial. These different social patterns were connected with the different experiences made by the cats during ontogenesis: Kittens growing up with social conspecifics became social, whereas kittens growing up with non social cats usually became nonsocial, i.e. the socialization of the individuals depended on the type of conspecifics being present at the subadult stage.

Thus the limiting of social partners and the elimination of social or nonsocial cats by the farmers, who generally control the size of their cat colony, do influence the socialization of kittens and thus also the social structure of groups.



# **Effects of special skills of individuals in a *Macaca fascicularis* group on social interactions and organization**

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A group of longtailed macaques (*Macaca fascicularis*) was trained to obtain a popcorn reward from an apparatus by manipulating one lever. When all the animals were habituated to the problem, in each of three replicates one monkey only was taught to pull three levers in a correct sequence and thus became the 'specialist' for producing popcorn. The other monkeys first had to learn that their manipulations of this apparatus were not successful and, later on, began to treat the specialist in a different way than they did before: He was no more chased away from the apparatus; in one of the replicates, the highest ranking male chased other group members, except the popcorn producing specialist. Grooming interactions between the two animals increased, but decreased again when the specialist was replaced by another one. These experiments show that monkeys with special skills may improve their social relationships if other monkeys may benefit from their skills.

# **Behavioral and environmental causes of estrus in lactating sows**

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Observations on Large White domestic pigs kept in groups outside or in family pens indicated, that sows regularly exhibit lactational estrus in rich social and physical environments. In semi-natural enclosures estrus occurred in 20 of 25 lactations, and in enriched family pens in all 63 lactations,  $38 \pm 12$  days p.p. To assess the stimulatory factors of these environments, lactating Landrace sows were housed in three environments differing in complexity, i.e. crates, pens with optional yards and enriched family pens. As additional treatment factors different possibilities for locomotion, manipulation and contact to other sows, boars and piglets were provided. Effects on sow and piglet behavior were assessed by scanning and continuous observations. No sows have exhibited full lactational estrus in the crate and pen treatments, even if grouped sows were kept with a boar. In the family pens sows obtained more heat-enhancing stimuli, as they visited the areas outside the nest more frequently, showed more exploratory and social behavior, and also received less piglet stimuli. Thus, even the combined treatment factors induced lactational estrus only in a complex environment, which is not provided in conventional housing.

# **Effects of visual and auditory deprivation on the behavior of the albino mouse (*M. musculus*)**

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Male LACA mice were housed in enclosures of  $1.8 \times 1.8$  m<sup>2</sup>. After about 74 days some males defended individual territories. The significance of vision and audition on territorial behavior was tested on the basis of the following measures: total activity, length of the chase track, number of special attacks, number of successful and unsuccessful attacks. Visual deprivation was carried out reversibly by providing the mice with opaque contact lenses; auditory deprivation by means of silicon rubber plugs. The results show, that during the detection phase (becoming aware of an intruder) audition is most important, vision is involved when short distances (below 10

cm) are considered. The tracking phase (chasing) is almost exclusively guided by audition, whereas the attacking phase is mainly visual. Further observations pointing towards olfaction as being primarily involved in the detection of static objects (orientation by scent marks) are under way.

# **The orientation of the golden hamster to its nest site: I. The use of allothetic information**

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Within the limited space of an experimental arena ( $\varnothing = 2.20$  m), golden hamsters carry food back to their peripherally located nest site by following a direct path. The role of allothetic (exteroceptive) information was tested by presenting or eliminating various sets of directional cues. Olfactory, auditory and geomagnetic information does not influence significantly the subject's orientation in conditions which involve the elimination of visual cues and a passive transportation of the subject to the food source. However, visual cues from outside the arena play a major role and predominate over information which the animal obtains by path integration. The nature and specific location of these cues within the animal's visual field have still to be determined.

# **Reactions of domestic cats to an unfamiliar person: comparison of mothers and juveniles**

D. C. Turner

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The behavior of 12 adult female cats and 11 juveniles towards an unfamiliar person was recorded in an encounter room at Cambridge University during each of three trials per cat over 3 days. All trials were run blindly. Three persons familiar with (and to) the cats independently ranked the animals on a scale of friendliness toward familiar persons. Using the rank sum of four behavioral measures of reaction to the unfamiliar person, an estimate of friendliness towards that stranger was made for each cat. No correlation between friendliness toward familiar persons and reaction to stranger was found. Older females reacted more positively to the stranger than younger adults. Mothers showed less variation in and somewhat more positive reactions to the stranger than their juveniles. Siblings raised by the same mother in the same environment, were capable of showing very divergent reactions to the stranger.

# **A universal model for symbolism**

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Until recently no universal model existed for all symbols. Two constant elements were known in them: the symbolizing *s*, and the symbolized *S*. Conceiving of them as elements of mathematical sets the author concludes that a *third element T* must exist. It relates a certain *S* to a subset *s'* by way of unique mapping. Together with elements of the body scheme and perceptual apparatus a tetradron structure can be assigned to any symbol. If associated with measurable magnitudes *m*, *n*, symbols like *LOVE* (heart beat), *ANIMA* (breath) and *SYMPATHY* (warmth) can be shown to constitute a pythagoraic triple:  $a = m^2 - n^2$ ,  $b = 2mn$ ,  $c = m^2 + n^2$ . They also define a unit circle for the coordinates ' $X = a/c$ ', ' $Y = b/c$ ' assigned to the symbol associated with the *m*, *n*. Depending upon the mode of mapping three classes of symbols ensue: by substitution (object/object); by modus (color, space symbolism); by synthesis (the *SHADOW*, the *STRANGER*, combinatory *FIGURES*).



## Insect behavior (Prof. Dr G. Benz)

### Analysis of the breeding behavior of the fossorial wasp, *Sphex albisectus* Lep. (Hym., Sphecidae)

G. Benz

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The females of the fossorial wasp, *Sphex albisectus* Lep., dig vertical tunnels leading to a horizontal brood chamber in sandy dirt roads (e.g. in the Valais). They place one large or two smaller paralyzed grasshoppers in each brood chamber and lay one egg in it. The breeding behavior is an inborn sequence of more than a dozen different actions, each one released by its specific key factor while the insect exhibits a specific appetitive behavior. If two grasshoppers are hunted a large subsequence has to be repeated. Indeed, in some phases of the complex behavior a great plasticity and an astonishing power of learning can be observed, sometimes even suggesting intelligent behavior. – Based on some experiments it is demonstrated that all actions are stereotype that guarantee success, whereas the behavior is flexible when adaptation to varying conditions is necessary for successful breeding. However, it can be shown that intelligent behavior does not occur.

### *Apis mellifera* and weather – a quantitative study on bee traffic at the hive entrance

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At the entrance of a normal free flying honeybee colony, the number of passing bees was monitored by a newly developed electronic device. In June 1983, when the number of adult bees in the colony was about 18,000, the number of passages per day ranged from 46,000 to 309,000. Bee traffic ceased between 20.00 h and 21.40 h and resumed between 04.20 and 06.40 h. On sunny days, there was a slight depression of the rate of passages around noon.

The same colony was continuously surveyed for several months. By comparison with the records from the nearby meteorological station, the relative contribution of the different meteorological factors and their interactions affecting honeybee traffic at the hive entrance can be examined. Obviously, non-meteorological factors (e.g. nutrition) also play an important role.

### Inversion polymorphism: a way to keep a pool of different behavior in a wild population?

H.E. Jungen

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The unusual high degree of inversion polymorphism in *Drosophila subobscura* is still not fully understood. This contribution gives evidence for a correlation between frequencies of specific inversions and behavior such as flight or feeding activities.

Males were trapped every half day in the Valais. The analysis of the salivary gland chromosomes in the offspring revealed significant temporal changes in the gene arrangement frequencies. At least three out of the five large chromosomes were involved. In the J chromosome the  $J_{ST}$  dropped from 59% to 30% and in the U chromosome  $U_{ST}$  decreased from 50% to 22% within 24 h. A recovery followed, reaching again the originally frequencies after 12–36 h. The frequency shifts were

probably connected to the meteorological situation, for at the end of this period a weather front passed with thunderstorm and rain.

### Division of labor in higher termites

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Caste and age polyethism was observed in the social organization and food processing in the fungus growing termite colony *Macrotermes* sp. Major workers participate predominantly in foraging, minor workers in nest building. Other functions are performed by both castes according to an age schedule. Young workers (< 30 days after emergence) eat the harvested dry grass, produce primary feces to build up the fungus substrate, eat the nitrogen-enriched fungus noduli, have their feeding glands activated and nurse the offspring. Older workers (> 30 days after emergence) harvest the food, eat the exspired fungus comb material, feed the soldiers, eat carcasses and produce final feces. These observations were made in laboratory colonies and confirmed in the field.

### Coexisting patterns and foraging behavior of ants on giant cacti on three Galapagos Islands, Ecuador

R.E. Meier

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Extrafloral nectaries on giant cacti (*Opuntia echios*) of the arid zone represent a rich and stable foodsource for many soilnesting ants. During garúa season (September to December) foraging and feeding ants on cacti were observed on Isla Santa Cruz, Santa Fé and Daphne Major. *Wasmannia auropunctata*, *Paratrechina vaga* and *Tetramorium guineense*, all tramp species, and the endemic *Camponotus planus* often foraged alone, while *P. longicornis*, *C. macilentus*, *Dorymyrmex pyramicus*, *Monomorium floricola* often coexisted with sympatric ants. 24 h observation of some cacti revealed *W. auropunctata* and *P. longicornis* to be active day and night, while *M. floricola* was active during day and *C. macilentus* during night only. The recruitment velocity of *W. auropunctata* in mass trails was increased compared to small trails; this effect may be due to a pheromone. The logistic support by the Darwin Station and the Servicio Parque Nacional Galapagos is appreciated.

### Interference behavior of two tramp ants (Hymenoptera: Formicidae) at protein baits on the Galapagos Islands, Ecuador

R.E. Meier

Kantonsschule Stadelhofen, CH-8001 Zürich

At Darwin Station, Isla Santa Cruz, where the introduced little fire ant (*Wasmannia auropunctata*) is abundant, only few ant species can coexist. In an area of overlap with another tramp species (*Paratrechina longicornis*) at tunafish baits competition behavior was studied. The recruitment and defensive patterns of foraging worker ants of either species were observed up to 45–60 min. Often the 2.5 times bigger and 10 times swifter *P. longicornis* fled *W. auropunctata* even without tactile contact. *W. auropunctata* occupied baits were experimentally shifted near nesting sites of *P. longicornis*. The powerful interference of *W. auropunctata* depended rather on repellent pheromone effects than on aggressive strategies, e.g. on its painful sting or

its mandibles. This dominance could be due to alkylpyrazine from the mandibular glands of *W. auropunctata* which in laboratory studies attracted disturbed workers and repelled other species in Florida (Howard et al., Insect. Soc. 29 (1982) 369).

### **Honeybees maximize efficiency by not filling their crop**

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Zoologisches Institut, Universität Basel, Rheinsprung 9,  
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Nectar-gathering honeybees (*Apis mellifera* L.) often abandon nondepleting food sources with a partially filled crop. This behavior contradicts predictions of widely used foraging models. We show that by including the additional metabolic costs of carrying a nectar load, models based on energetic criteria predict partial crop loading. Furthermore, the observed crop loads are not consistent with maximization of delivery rate to the hive, but can be predicted by maximization of energetic gain per unit of energy spent. This behavior may be an adaptation to a limited flight-time budget and related to the social habit of the honeybee.

### **Host selection behavior of herbivore insects influenced by specific compounds of the host plant leaf surface**

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In leaf feeding insects constituents of leaf surface waxes release the first biting or probing which gives access to the interior of the leaf providing essential information on its identity and nutritional value. Oviposition females can often not rupture the leaf, thus the surface structure and chemistry is the only information available for the identification and evaluation of potential host plants. The behavior of these insects prior to biting or oviposition seems to be adapted for an optimal 'sampling' of the leaf surface with different sensory organs. Examples for such sensory organs are the contact chemoreceptors on the tarsi sensitive to polar, nonvolatile compounds, receptors for leaf wax components on the maxillary palpi and the olfactory receptors on the antennae sensitive to compounds present in the boundary layer of the leaf.

### **Nest temperature control and social behavior in colonies of the paper wasp, *Polistes biglumis himaculatus* (Hymenoptera, Vespidae)**

R. Staub  
Kantonsschule Zürcher Oberland, CH-8620 Wetzikon

The effect of temperature regulation in paper wasps by fanning the nest surface by means of whirling wing movements and distributing water drops into the cells was measured with air-thermocouples within single cells and documented on super-8-film. Some experiments with artificially overheated nests showed the predominance of the founding female (foundress) in water distributing behavior whereas most worker wasps continued fanning. Slow motion film sequences on trophallaxis of color marked individuals illustrated the well-known begging versus food offering behavior within a certain colony hierarchy. A correlation between age and rank among workers, as first suggested by Pardi, relying upon other criteria (Boll. Ist. ent. Univ. Bologna 15 (1946) 25), could not be established by these observations.

### **Web building and the construction rules of an orb-weaving spider**

F. Vollrath  
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The orb-weaving spider uses certain rules to guide its movements during web construction. Information about the state of the web and the position of body and legs provide the animal with the cues necessary for the implementation of these rules. Experimental interference with a crucial parameter like gravity confuses the animal and leads to the construction of abnormal webs.

### **Artificial intelligence (Prof. Dr E. Engeler)**

#### **Computer modelling of mathematical reasoning**

A. Bundy  
University of Edinburgh, Scotland

How does an experienced mathematician pick his way through the bewildering array of possible steps to construct the proof of a theorem? Can this experience be captured in a computer program for proving theorems? We investigate these questions in the domain of solving nondifferential, symbolic equations, such as those encountered in a pre-university mathematics course. By investigating successful attempts to solve equations we uncover a language for describing algebraic expressions and solution methods, and these form the basic of an equation solving program, PRESS. Is there any correspondence between the processing of PRESS and the thought processes of experienced mathematicians? If so, can PRESS be used to help teach algebra?

### **The space of possible minds**

A. Sloman  
University of Sussex, England

There is a vast space of possible computational systems, whose structure is barely understood at present. It is not a continuum, for there are important discontinuities, and it is not one-dimensional, since any system may be altered in a variety of different ways to form new systems. By exploring this space, studying different sorts of computational mechanisms, studying the general principles underlying processes such as perceiving, inferring, learning, planning, comparing, deciding, acting, interrupting an action, etc. we may hope to gain an understanding of many different sorts of behaving systems, including thermostats, amoebas, mice, chimpanzees, human beings, and intelligent machines yet to be constructed. This study requires the techniques of artificial intelligence to be combined with many other disciplines, including psychology, neurobiology, linguistics, logic, philosophy, ethology, mathematics and computer science. Besides helping us design new intelligent systems, this study should also provide, at last, a general conceptual framework for investigation natural intelligent systems, and their evolution. For instance, we may hope to learn how emotional states are to be expected in systems capable of acting intelligently in our world.

## Demonstration – the Sussex University POPLOG system

A. Sloman

University of Sussex, England

POPLOG is an integrated, portable, interactive software development environment, including incremental compilers for PROLOG, LISP and POP-11 (a LISP-like language, with a syntax more like PASCAL). The demonstration showed how

the screen editor VED could be used as an interface to the different compilers, to the on-line help system, to the teaching files, etc. and how, by working within such a system, the normal cycle of editing, compiling, linking, testing and debugging could be enormously speeded up. The use of pattern-matching and list-processing in POP-11 and logic programming in PROLOG were briefly illustrated. POPLOG is widely used for teaching and research in artificial intelligence, but can be used for more general software development purposes.

## Announcements

### Portugal

#### 9th world chromatography/7th world spectroscopy conference

Funchal, Madeira, 12–13 May 1986

Information by Dr V.M. Bhatnagar, ALENA Enterprises of Canada, P.O. Box 1779, Cornwall, Ontario K6H 5V7, Canada.

### Federal Republic of Germany

#### IXth international congress of infectious and parasitic diseases

Munich, 20–26 July 1986

The theme of the congress is: Progress and future trends in infectious and parasitic diseases. Information through the Congress Secretariat, Mrs C. Schäfer, Abteilung Infektions- und Tropenmedizin der Universität, Leopoldstrasse 5, D-8000 München 40.

### Switzerland

#### Friedrich Miescher Award 1986

To commemorate the 100-year anniversary of the discovery of nucleic acids the Swiss Biochemical Society has created the Friedrich Miescher Award. This annual prize is donated by the Friedrich Miescher Institute of Ciba-Geigy Inc., and is intended to honor young biochemists of high scientific caliber.

Excerpts from the statutes:

- 1) The Friedrich Miescher Award will be awarded once annually to a young scientist for outstanding achievements in biochemistry.
- 2) Preference will be given to candidates not older than 35 years. Eligibility extends only to candidates not exceeding their 40th year.
- 3) The scientific work must have been carried out in Switzerland or by Swiss scientists abroad.

Applications or nominations of candidates born 1947 or later should be submitted by **November 1, 1985** to the secretary of the Swiss Society for Biochemistry: PD Dr A. Jakob, Department of Biochemistry, University of Basel, Vesalianum, Vesalgasse 1, CH-4051 Basel/Switzerland.

## Instructions to Authors

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**Mini-reviews** (1–2 printed pages)

**Short Communications** (1–2 printed pages)

Papers reporting on work that is preliminary in nature, or wherein animal experiments have been conducted without the appropriate anesthesia, will not be accepted.

Manuscripts (including all tables and figures) must be submitted in triplicate and must be in *English*. *Title pages* should bear the author's name and address (placed directly below the title), a brief *abstract* (of approximately 50 words for short communications) mentioning new results only, and a listing of *key words*. *Footnotes* must be avoided. *Tables*, and then *figures*, are to follow the body of the text and should be marked with self-explanatory captions and be identified with the author's name. All *data* should be expressed in units conforming to the *Système International* (SI). *Drawings* are to be on heavy bond paper and marked clearly in black. *Photographs* should be supplied as glossy positive prints. Please note that we use two different systems for citing references. 1. For *Review Articles*, references should be arranged alphabetically and be numbered. Within the text, literature should be referred to by number and, where indicated, by author. The references should contain full journal article titles and the first as well as the last page of the article cited. 2. For *Short Communications*, an abbreviated bibliography is requested and references should be listed chronologically. Please consult a current issue of *Experientia* or inquire at the editorial office for details on form.

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