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Seasonal changes in the hypothalamic vasopressinergic system of a wild Sahelian rodent, *Taterillus petteri*

Frédéric Fuminier[1, 2], Bruno Sicard[1, 2], Line Boissin-Agasse[2], Jean Boissin[2]

[1] Centre ORSTOM, B.P. 182, Ouagadougou, 01-Burkina Faso
[2] Laboratoire de Neurobiologie endocrinologique, URA 1197 CNRS, Université de Montpellier-2, Place Eugène-Bataillon, F-34095 Montpellier Cedex 5, France

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Abstract. Seasonal variations in the immunoreactivity of vasopressinergic perikarya in the paraventricular (PVN), supraoptic (SON) and suprachiasmatic nuclei (SCN), and in the labelling of vasopressinergic fibres in the internal zone of the median eminence were studied in *Taterillus petteri*, a rodent that is found in the north Burkina Faso (formerly Upper Volta). In this region, there are four seasonal climatic combinations: the humid and hot, humid and cold, dry and cold, and dry and hot seasons. In the dry hot season, the rodents experience phases of torpor (adaptation to dryness). Immunoreactivity of the PVN and SON is highest during the dry cold season. Labelling is intense during the dry hot and humid hot seasons, and is at its lowest during the humid cold season. In the SCN, labelling of the perikarya is only dense during the dry hot season, whereas for the rest of the year, the immunoreactivity is weak or undetectable. The pattern of immunoreactive variations of vasopressin-positive fibres located in the internal zone of the median eminence is similar to those of vasopressinergic perikarya in the PVN and SON. These results suggest that there is an association between: (1) seasonal modifications in the immunoreactivity of PVN and SON vasopressinergic perikarya and vasopressinergic fibres of the internal median eminence, and (2) climatic conditions, water metabolism, behavioural activity and diet. It is not possible to establish a correlation between seasonal variations in water availability and fluctuations in the labelling of vasopressinergic perikarya in the SCN. However, labelling is intense when the animals are in torpor during the dry hot season.

Key words: Vasopressinergic system – Paraventricular nucleus – Supraoptic nucleus – Suprachiasmatic nucleus – Median eminence – Immunohistochemistry, semiquantitative – Aestivation – Lethargy – *Taterillus petteri* (Rodentia)

Correspondence to: J. Boissin

Introduction

A feature of rodents living in dry inter-tropical regions is that throughout the year they aestivate. Aestivation is characterized by a striking decrease in general locomotor activity outside the burrow and successive phases of torpor. *Taterillus petteri* is a newly discovered member of the family Gerbillidae (Sicard et al. 1988); it lives in dunes in the far northern part of the Sahel of Burkina Faso (formerly Upper Volta) (14°20′N–14°50′N and 0°10′W–0°40′W). It aestivates from the end of February to the end of May, during the dry hot season (Sicard 1987).

An analysis of annual variations in water turnover and water balance in relation to aestivation and locomotor behaviour in wild *T. petteri* has shown that the beginning of phases of torpor is preceded by a change in the water balance; this occurs in January–February during the dry cold season (Sicard and Fuminier 1992). Enough food is available during this dry cold season to cater for the increase in requirements generated by high energy expenditure resulting from an increase in general locomotor activity. The equilibrium of the water balance is then re-established during aestivation, and thus plays an adaptive role.

The physiological mechanisms that control the initiation and termination of aestivation are still unknown, but it has been suggested that initiation might be triggered by water deficiency, which is characteristic of January–February. We have thus investigated possible immunoreactive variations in vasopressinergic perikarya situated in the paraventricular (PVN), supraoptic (SON) and suprachiasmatic nuclei (SCN), and in vasopressinergic nerve fibres present in the internal zone of the median eminence.

Vasopressin plays an essential role in regulating water metabolism but it has also been detected in brain regions outside the classical neurosecretory system that serve neurohypophyseal antidiuretic functions (Dreifus 1989). This central vasopressinergic system could be involved in the regulation of the annual cycle of hypothermic

lethargy in hibernating mammals that live in temperate regions (reviewed in Pévet et al. 1989). Vasopressin may therefore play a neuromediatory role (Dreifuss 1989). It is equally important to note that the vasopressinergic system projects to the internal median eminence and that the central vasopressinergic innervation originates in the same hypothalamic nuclei (PVN, SON and SCN) (Buijs 1978, 1990; De Vries and Buijs 1983; Lang et al. 1983; Hawthorn et al. 1985).

In the present study, we have analysed the changes in the immunoreactivity of vasopressinergic perikarya located in the PVN, SON and SCN, and of vasopressinergic nerve fibres present in the internal zone of the median eminence. These changes are related to seasonal variations in water metabolism and locomotor activity (Sicard 1987; Sicard and Fuminier 1992).

Materials and methods

Regional climate

The study was carried out in the region of Oursi (14° N) situated to the north of Burkina Faso. The regional climate is typically Sahelian, and is characterised by 4 seasons: the humid and hot season (from June to September), the humid and cold season (October and November), the dry and cold season (from December to February), and the dry and hot season (from March to May).

Animals

Taterillus petteri (Gerbillidae) is a newly identified species with a karyotype of 2n = 17–18 chromosomes (Sicard et al. 1988). Animals were captured using Chauvancy traps (Licence CNRS), placed in lots of 100 for each trapping session on old arid dune cordons, the natural habitat of *T. petteri*. Trapping sessions was regularly carried out over the four seasons. During aestivation, animals were captured by digging up burrows or by placing traps at the entrances to the burrows during periods of activity. Aestivation is made up of an irregular series of periods of torpor vs activity outside the burrow; this is similar to the daily torpor of the Djungarian hamster (Ouarour 1991).

Immunohistochemical procedures

Captured animals were classed by sex and age as a function of their sexual maturity (adults, sub-adults, and juveniles), as estimated (in the case of males) by their testicular volume. The brains of 5 adult males were removed and fixed at the site of capture during each capture session as follows. After deep Equithesin anaesthesia (intraperitoneal injection of 0.4 ml Equithesin), animals were perfused through the heart with phosphate-buffered saline (PBS) (8 g of NaCl, 0.2 g of KCl, 1.44 g of Na_2HPO_4, and 0.24 g of KH_2PO_4 in 800 ml of distilled water, adjusted to pH 7.4 with HCl; H_2O added ad 1 l), followed by a fresh solution of 4% paraformaldehyde in 0.1 M phosphate buffer (pH 6.9) containing 0.2% picric acid. Brains were then removed from the skull and postfixed for 12 h in the perfusion fixative. For long-term conservation, brains were soaked in 0.1% sodium azide in PBS at 4° C, then rinsed for 18 h in PBS containing 10% sucrose, and finally frozen in liquid nitrogen. Frontal sections (10 µm thick) were cut in a cryostat and serially thaw-mounted on gelatin-coated histological slides. Mounted sections were treated for indirect immunofluorescence microscopy as previously described (Boissin-Agasse et al. 1988). Briefly, sections were incubated for 18 h in a humid atmosphere with primary antibody (anti-vasopressin raised in our laboratory) diluted 1:200, and then for 3 h with a secondary antibody conjugated to fluorescein isothiocyanate diluted 1:100. Antibodies were diluted in PBS containing 0.2% gelatin.

The specificity of the labelling was verified by incubating control sections (1) with secondary antibody alone, and (2) with primary antibody preabsorbed for 4 h at ambient temperature with the corresponding synthetic peptide (0.5 mg/ml diluted antiserum) (Alonso 1988).

Immunostaining analysis

Immunofluorescent-labelled sections were photographed at an exposure of 30 s (under a HBO 200 high pressure mercury lamp, using a 515 nm excitation filter, at ×16 magnification). Film (X Kodak, 400 ASA) was developed for 11 min at 20° C in freshly prepared developer (Microphen) and fixed for 10 min in Ilford rapid fixer. In all cases, the sections for photography were freshly prepared, and the same times and conditions were used.

Semi-quantitative values for vasopressin labelling were obtained by measuring the optical density (OD) as previously described (Boissin-Agasse et al. 1991). An average of 10 sections (10 µm thick) from each animal were analysed. The negatives were placed in an illuminated viewing box (the negatives were all processed in a single session and under identical conditions) and ODs (grey-tone values) were read with a semi-automatic analyser (DATA-SUD system) coupled to an HP computer. The ODs obtained were corrected for background by subtracting the ODs of unlabelled reference areas of the sections. The labelled areas of perikarya and median eminence axon endings were also read. The labelled surface area (LA), defined as the area of the section with an OD greater than that of the reference sections, was automatically calculated by an in-house program.

OD and LA were expressed as means ± SEM. For statistical comparisons, we used a one-way ANOVA test followed by Student's *t* test.

Results

Vasopressin is mainly synthesized in the magnocellular neurons of the PVN (Fig. 1) and SON (Fig. 2) and in certain parvocellular neurons of the SCN (Fig. 3). Magnocellular neurons are evenly spread throughout the PVN and SON, whereas SCN parvocellular neurons have a peripheral distribution. These small neurons are disposed around the external circumference of the nucleus.

The immunoreactivity of vasopressin-containing perikarya located in the PVN (Fig. 1), SON (Fig. 2) and SCN (Fig. 3) displayed large seasonal variations. Nevertheless, the PVN and SON were strongly labelled throughout the year. In contrast, the SCN was intensely labelled only in samples taken during the dry hot season; for the rest of the year, SCN labelling was extremely weak, and sometimes undetectable.

Immunoreactivity of vasopressinergic fibres present in the internal zone of the median eminence was also subject to variations throughout the year (Fig. 4). Two parameters were measured: the OD of labelled areas and the immunolabelled area as a percentage of the standard unlabelled area (LA).

The profile of seasonal variations in the immunoreactivity of vasopressin-containing perikarya situated in the PVN (Fig. 4A) was the same as that in the SON (Fig. 4B). These variations were comparable to those

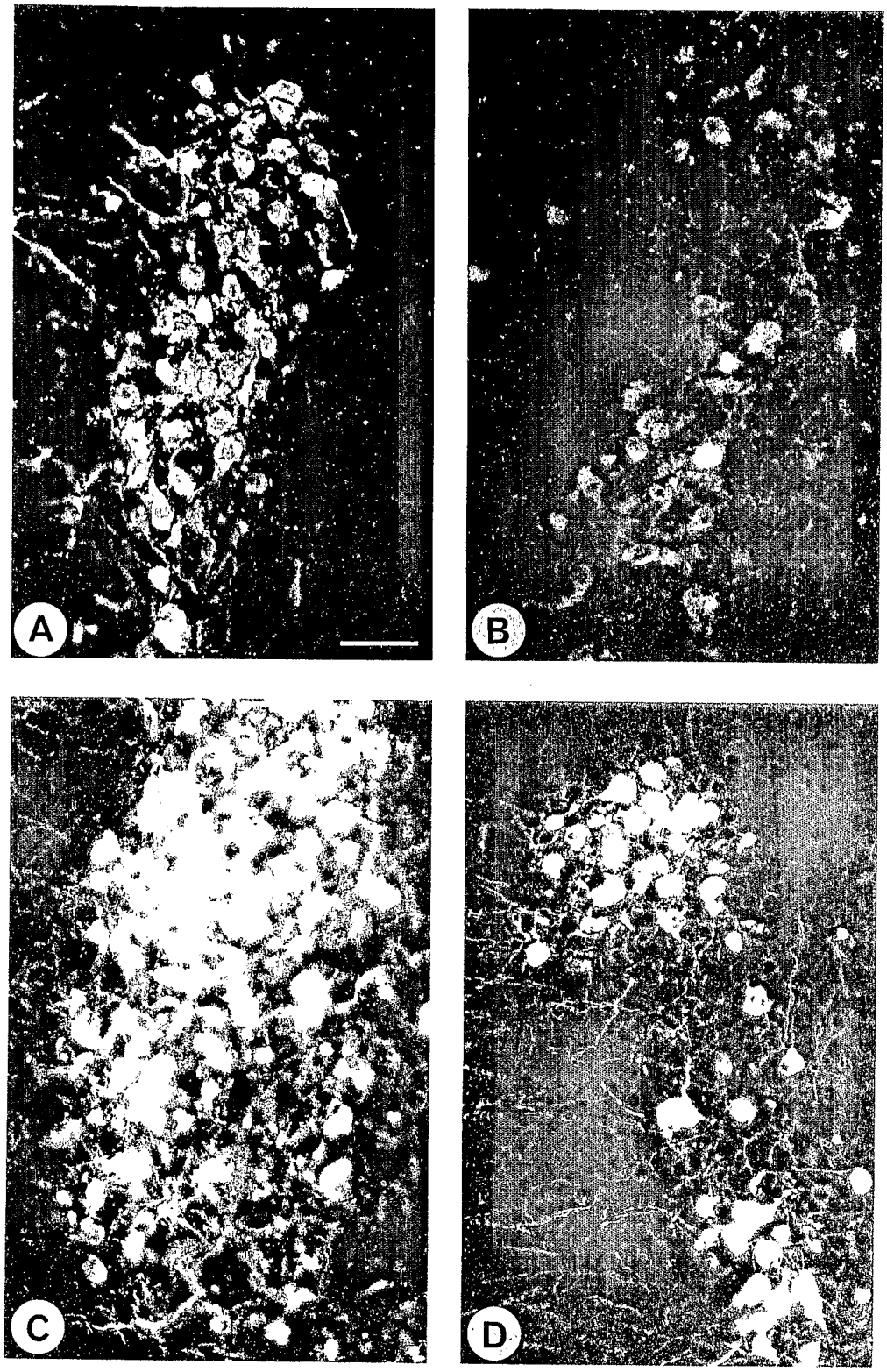

Fig. 1A–D. Frontal sections through the paraventricular nucleus of *Taterillus petteri* after incubation with antiserum to vasopressin. Seasonal variations in the immunolabelling of vasopressinergic perikarya are observed. Animals were killed during the humid hot season (A), the humid cold season (B), the dry cold season (C) and the dry hot season (D). *Bar*: 50 μm

in the internal zone of the median eminence (Fig. 4D). The pattern of variations observed in the SCN was different (Fig. 4C).

The PVN and SON were most strongly labelled during the dry cold season (PVN: OD = 290 ± 45, I.A = 4.7 ± 1.2; SON: OD = 1150 ± 46, I.A = 28.0 ± 2.1); this was not significantly different from the values in the dry hot season (PVN: OD = 247 ± 35, I.A = 3.9 ± 0.

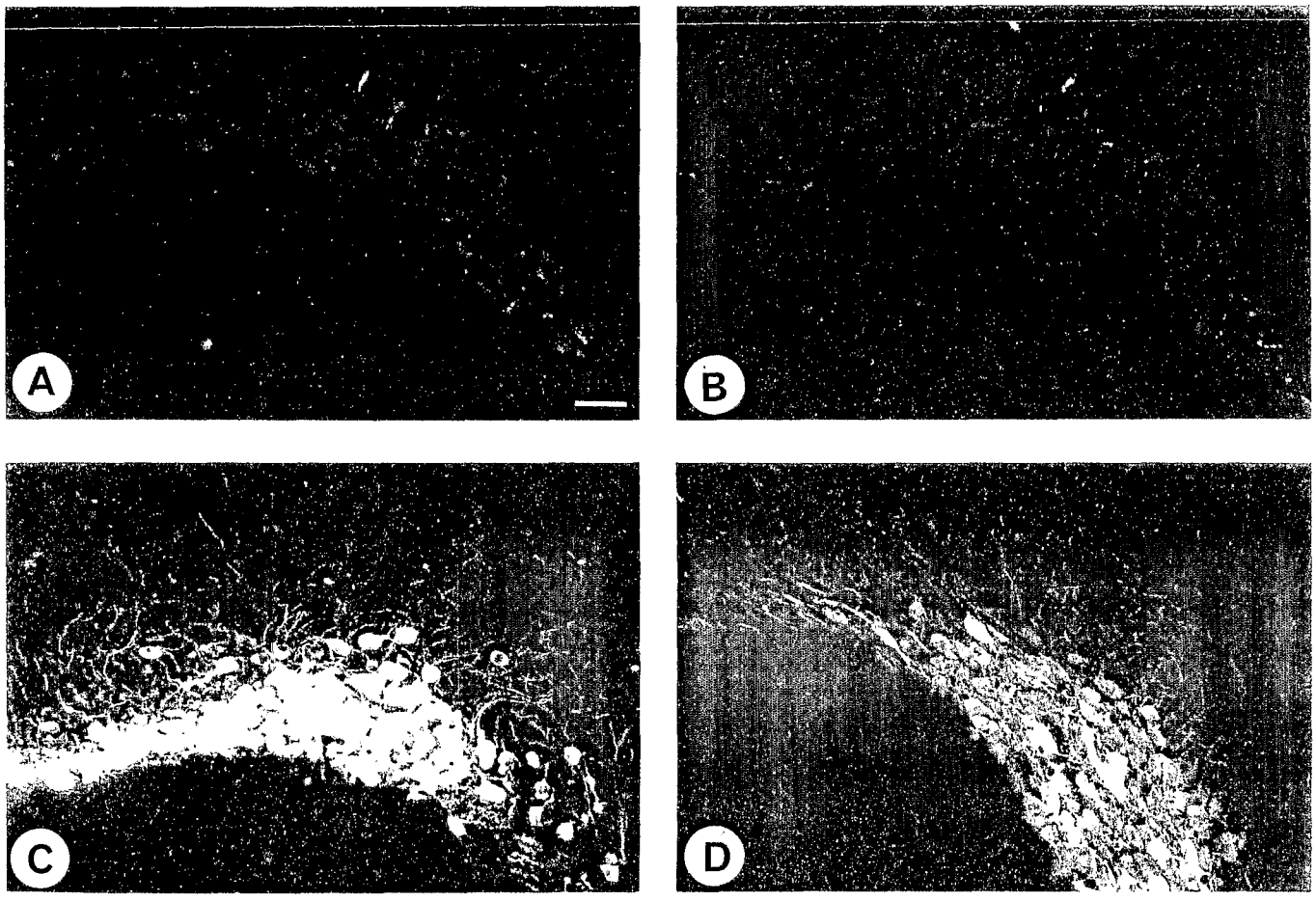

Fig. 2A–D. Frontal sections through the supraoptic nucleus of *Taterillus petteri* after incubation with antiserum to vasopressin. Seasonal variations in the immunolabelling of vasopressinergic perikarya are observed. Animals were killed during the humid hot season (A), the humid cold season (B), the dry cold season (C) and the dry hot season (D). *Bar* 50 μm

SON: OD = 929 ± 61, LA = 16.1 ± 4.0) and the humid hot season (PVN: OD = 225 ± 20, LA = 2.5 ± 0.4; SON: OD = 665 ± 29, LA = 22.4 ± 2.3). The values for the humid cold season were significantly lower ($P < 0.01$) (PVN: OD = 101 ± 13, LA = 1.6 ± 0.2; SON: OD = 380 ± 12, LA = 9.0 ± 0.8).

In the case of the SCN (Fig. 4C), labelling of the perikarya was only dense during the dry hot season (OD = 99 ± 55, LA = 6.3 ± 4.2). During the other three seasons, the immunoreactivity of the SCN was very weak

Vasopressin-positive nerve fibres present in the internal median eminence were most intensely labelled during the dry cold season (OD = 1692 ± 160, LA = 22.7 ± 2.8). Immunoreactivity was lower during the dry hot season (OD = 1370 ± 140, LA = 2.76 ± 2.8), but the difference observed between the dry cold, and dry hot seasons was statistically not significant. During the humid hot season, labelling was less intense (OD = 1030 ± 51, LA = 19 ± 2.5), and these values were significantly lower ($P < 0.01$) than those for the dry cold season. Immunoreactivity of vasopressinergic endings was minimal during the humid cold season (OD = 712 ± 45, LA = 12.4 ± 2.4).

Discussion

The immunoreactivity of vasopressin-containing hypothalamic perikarya is subject to considerable seasonal variations in *Taterillus petteri* living in its natural environment. The variations are particularly significant in the PVN and SON. The same pattern of variation is observed in these two nuclei: the changes in the labelling of vasopressinergic fibres in the internal zone of the median eminence are similar.

The immunoreactivity of vasopressin-containing perikarya in the SCN is only significant in March to May (dry hot season), and is practically undetectable during the rest of the year.

The PVN, SON and their axonal endings located in the median eminence are most strongly labelled during the dry cold season (December to February); labelling is also intense during the humid hot (June to September) and dry hot (March to May) seasons. The cell bodies are only weakly labelled during the humid cold season (October to November).

The immunocytochemical techniques used do not distinguish between increased synthesis and reduced release leading to stockpiling of vasopressin in the perikarya. However, the increase in the number of labelled fibr-

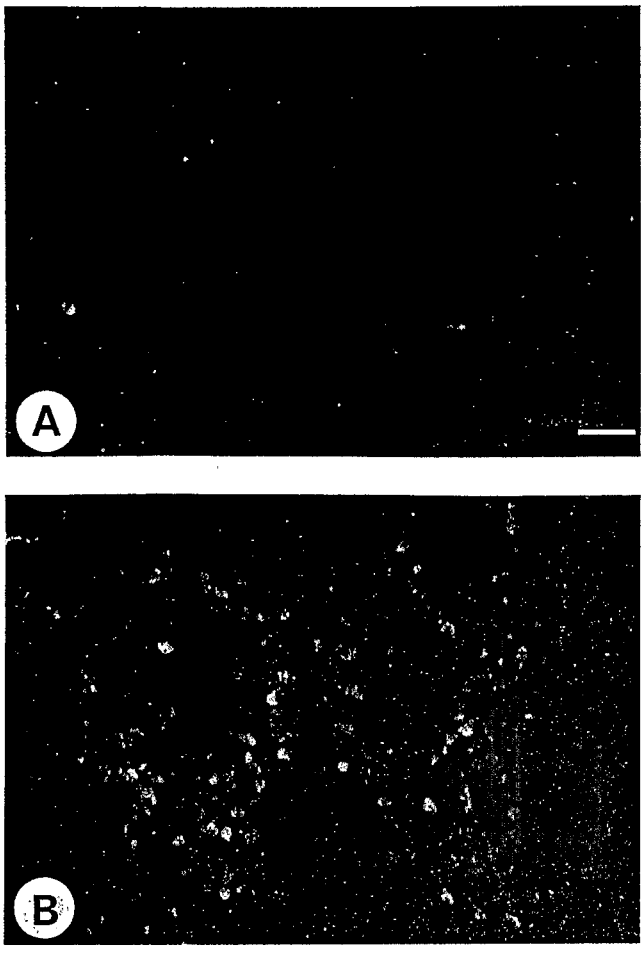

Fig. 3A, B. Frontal sections through the suprachiasmatic nucleus of *Taterillus petteri* after incubation with antiserum to vasopressin. The immunoreactivity of the parvocellular vasopressinergic neurons is much higher during the dry hot season than the rest of the year. Animals were killed during the humid hot season (**A**) and the dry hot season (**B**). *Bar*: 50 μm

is concomitant with the increased intensities of labelling in the internal zone of the median eminence. This pattern is consistent with both an increased synthesis of vasopressin and an increased release.

It has been shown by assaying the mRNA encoding vasopressin that the SON and PVN respond similarly to plasma osmotic changes: osmotic stimulation leads to an increase in the levels of vasopressin mRNA (Uhl et al. 1985; Majzoub et al. 1987).

The dense labelling of vasopressin-containing perikarya and nerve fibres may indicate an antidiuretic state. Were this the case, the climatic conditions that determine the highest degree of aridity (dryness and high tem-

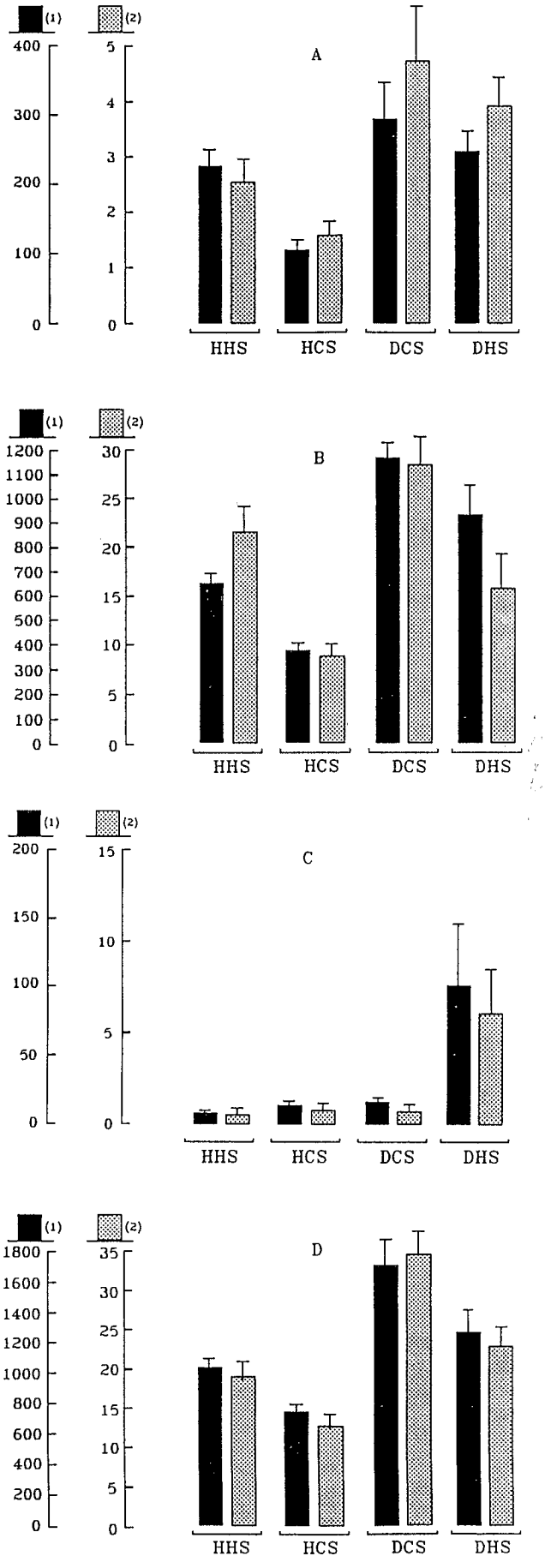

Fig. 4. Seasonal variations in the vasopressin immunostaining of perikarya in the paraventricular (**A**), supraoptic (**B**) and suprachiasmatic (**C**) nuclei, and in axonal endings in the internal median eminence (**D**). (*1*) Optical density per immunolabelled area unit; (*2*) immunolabelled area as % of the area of the zone in which the perikarya and fibres are located; HHS humid hot season; *HCS* humid cold season; *DCS* dry cold season; *DHS* dry hot season

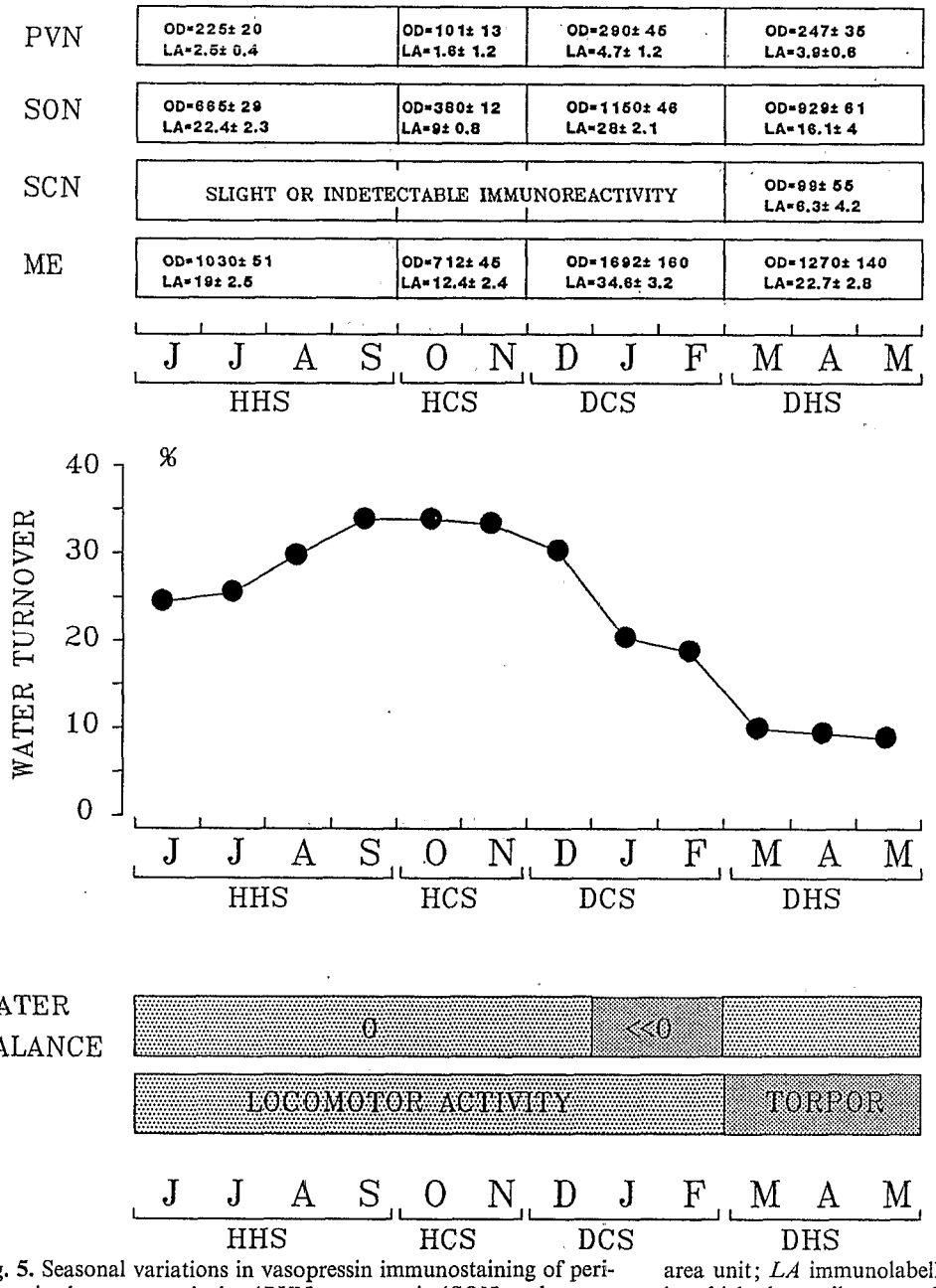

Fig. 5. Seasonal variations in vasopressin immunostaining of perikarya in the paraventricular (*PVN*), supraoptic (*SON*) and suprachiasmatic (*SCN*) nuclei, and in axonal endings in the internal median eminence (*ME*), considered in relation to water metabolism and locomotor activity. *OD* Optical density per immunolabelled area unit; *LA* immunolabelled area as % of the area of the zone in which the perikarya and fibres are located; *HHS* humid hot season; *HCS* humid cold season; *DCS* dry cold season; *DHS* dry hot season

peratures in March to May) were not those that lead to a spectacular stimulation of the vasopressinergic system in order to reduce urinal water loss. This indicates the adaptive role of the torpor phase, which coincides precisely with the driest period (Fig. 5) (Sicard 1987). This change of behavioural rhythm plays an essential role in maintaining a constant level of osmolality, since the animals exhibit a marked water deficiency at the start of the dry hot season (Fig. 5) (Sicard and Fuminier 1992). The phase of water imbalance (January to February), which precedes the driest period, corresponds to the strong immunoreactivity of vasopressin-containing perikarya in the PVN and SON, and of vasopressin-containing fibres in the median eminence. The term "water balance", as used by Schmidt-Nielsen and Haines (1964), indicates the status of the water reserves of the organism and is calculated by counting the remaining administered tritiated water and comparing the values at 3-day intervals (Sicard and Fuminier 1992). The intense labelling could be interpreted as a signal indicating the initiation of antidiuresis, in order to readjust the water balance. The study of seasonal variations

in water turnover has shown that it decreases substantially during the dry cold season (Sicard and Fuminier 1992) when the animals display a high level of locomotor activity because of pre-aestival burrowing (Sicard 1987).

The diet at this time of the year is exclusively granivorous. It has been shown that, in the case of *T. petteri* (Sicard and Fuminier 1992) and of other desert rodents (*Meriones shawii, Meriones libicus*: Bradshaw et al. 1976; *Dipodomys nelsoni, Dipodomys merriami, Perognathus penicilatus*: Grenot and Serrano 1979), the quantity of water in their diet strongly influences water turnover. Thus, water turnover is increased by herbivorous diets, and correspondingly reduced by granivorous diets.

Inversely, during the humid cold season (October–November), labelling of the neuronal perikarya in the PVN and SON and of the axonal endings in the median eminence is weak, whereas water turnover is very high. The locomotor activity during this part of the year is low, and the diet exclusively herbivorous.

These results suggest a causal relationship between (1) variations in climate conditions, water metabolism, behavioural activity and diet, and (2) the seasonal modifications of immunoreactivity in the vasopressin-immunostained perikarya in the PVN and SON and nerve fibres in the internal median eminence (Fig. 5).

The immunoreactive variations in vasopressin-containing perikarya located in the SCN have a different relationship to the climatic parameters, water metabolism and locomotor activity. Vasopressinergic labelling of the neuronal somata in the SCN is only dense during the torpor phase, when the water balance is in equilibrium (Fig. 5). It is thus difficult to establish a relationship, in *Taterillus petteri*, between the variations in labelling occurring in the SCN and the adaptation of the water metabolism to seasonal climatic changes. It is interesting to note that Zerbe and Palkovits (1984) have shown that, in the case of osmotic stimulation in the rat, the PVN and SON exhibit parallel changes in vasopressin levels, whereas the SCN and lateral septal nuclei are unaffected. Carter and Murphy (1989), on the other hand, in their study of the molecular mechanisms that regulate the expression of vasopressin-encoding genes in hypothalamic nuclei, have described an increase of cAMP levels in the SON and the PVN, but not in the SCN, during osmotic stimulation.

It is possible that changes in SCN vasopressin-immunoreactive perikarya are correlated to seasonal variations in locomotor activity. The level of immunoreactivity in *Taterillus petteri* is extremely weak throughout the year, but substantially increases during aestivation. Schindler and Nürnberger (1990) have shown that there is a large increase in the immunoreactivity of vasopressin-containing perikarya in the SCN of *Spermophilus richardsonii* during hibernation. The functional significance (if any) of SCN vasopressin in the regulation of the timing of the torpor phase is unknown.

Our results do not entirely validate the hypothesis proposing that the water balance deficiency observed in January and February represents an internal signal capable of initiating aestivation. It is, nevertheless, interesting to note that the highest degree of immunoreactivity of vasopressin-containing perikarya located in the PVN and SON is observed during the period that preceeds the beginning of torpor phases.

In hibernating mammals, vasopressin in the lateral septum is involved in the expression of various seasonal functions. Vasopressin immunoreactivity is intense in the lateral septum of the European hamster (Buijs et al. 1986) and the garden dormouse (Hermes et al. 1990) during the summer but is absent during the autumn and winter, during hibernation. Hamsters whose lateral septum has been infused with vasopressin show almost no periods of hypothermy (Hermes et al. 1989). Similar results have been obtained with the Siberian hamster, which normally shows diurnal phases of hypothermic torpor during the winter period (Ouarour 1991). Thus, a decrease in the levels of central vasopressin may be a prerequisite for hibernation or daily torpor in the Siberian hamster. It would therefore be interesting to analyse seasonal variations in the central vasopressinergic system of *Taterillus petteri* in relation to aestivation, with the aim to determine whether vasopressin plays analogous regulatory roles in hibernation and aestivation.

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