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1 Evans, Adv. Insect. Physiol. *15* (1980) 317.
2 Colhoun, E.H., Experientia *19* (1963) 9.
3 Cook, B.J., Raker, J.E., and Anderson, G.R., J. Insect Physiol. *15* (1969) 445.
4 Hiripi, L., and S.-Rózsa, K., J. Insect Physiol. *19* (1973) 1481.
5 Collins, C., and Miller, T., J. exp. Biol. *67* (1977) 1.
6 S.-Rózsa, K., and Miller, T., Adv. Physiol. Sci. *22* (1981) 557.
7 Brown, B.E., Gen. comp. Endocr. *5* (1965) 387.
8 Cook, B.J., and Holman, G.M., Comp. Biochem. Physiol. *61C* (1978) 291.
9 Cook, B.J., Int. J. Invert. Reprod. *3* (1981) 209.
10 Reinhard, J.F. Jr, Moskowitz, M.A., Sved, A.F., Fernstrom, J.D., Life Sci. *27* (1981) 905.
11 Véró, M., and Miller, T., Med. Biol. Eng. Computing *17* (1979) 662.
12 Dymond, G.R., and Evans, P.D., Insect Biochem. *9* (1979) 535.
13 Robert, A., Grillot, J.P., Guilleminot, J., and Raabe, M., J. Insect Physiol. *30* (1984) 671–684.
14 Miller, T., and James, J., J. Insect Physiol. *22* (1976) 981.
15 Brown, B.E., Life Sci. *17* (1975) 1241.
16 Robert, A., Grillot, J.P., and Raabe, M., C.r. Acad. Sci. Paris *293* (1981) 611.

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Both thermal and nociceptive afferents influence the unit activity of the neurons in the corpus striatum[1]

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Summary. Both thermal and nociceptive stimulation in the periphery were shown to influence the neuronal activity recorded in the striatal area. Both the thermal and nociceptive sensitvity of the striatal neurons were closely related.
Key words. Rat, striatum; striatum, rat; nociceptive afferents; thermal afferents; single-unit activity.

The striatum (caudate and putamen) receives dopamine-containing fibers arising from cell bodies in the zona compacta of the substantia nigra[2]. In addition, the striatum receives glutamate fibers from the cortex, serotonergic fibers from the dorsal raphe, and cholinergic inputs from the thalamic region[2]. The striatum in turn projects to the pallidum and to the substantia nigra zona reticulata[3]. The striatum is usually thought to be involved in the central control of motor performance. Recently, evidence has accumulated to suggest that striatal neurons are also involved in the regulation of thermoregulation[4,5] and the nociceptive reflex[6,7]. The present study was an attempt to assess the effects of thermal stimulation of scrotal skin and noxious stimulation of the tail on single unit activity in the striatum of urethane-anesthetized rats, to test whether or not there exist thermally responsive and/or nociceptive responsive units in the striatum.

Adult male Sprague-Dawley rats weighing between 250 and 300 g were used. Each animal was anesthetized with urethane (1.25 g/kg, i.p.). Supplementary doses were occasionally needed during an experiment. The rectal temperature was maintained between 36.8 and 37.5°C using a water-perfused pad under the animal. All the fur of the scrotum was removed with clippers. The animals were mounted stereotaxically with the heads fixed according to the König and Klippel coordinates system[8]. A piece of bone was removed from the right half of the skull and the underlying dura was removed. Recording of single unit discharges were made from the right half of the striatum at stereotaxic coordinates of A: 7.0–1.0; L: 2.0–3.6; and H: 2.0–0.0 mm[8]. Single-barrel micropipettes were filled with 4 M NaCl saturated with fast green dye and used for extracellular recording. The overall tip diameter of the micropipette was 2–5 μm. It generally had an impedance of 2–3 mΩ. After the micropipettes were lowered to the desired location in the striatum, a hydraulic microdrive was used to advance the micropipettes slowly. Single unit activity was processed using standard cathode follower and amplication circuitry for extracellular spike potential[9]. Impulses were counted at 1-sec intervals by WPI Scope Raster/Stepper Model 140 and displayed on a Grass polygraph recorder. Rectal temperature and scrotal temperatures were all displayed on the same polygraph record. The method used for thermal stimulation of the scrotum was similar to that described by Hellon and Misra[10]. Skin temperature was measured by a thermocouple connected to the surface of the thermode which was in contact with the skin. The noxious stimulation was produced by pinching the rat's tail with forceps.

A total of 77 single units in the striatal area were examined in 26 rats under urethane anesthesia. Each unit was subjected to change in scrotal temperature and to tail pinch (TP). Each unit was classified as either warm-responsive, cold-responsive or thermally unresponsive according to their thermal sensitivity. The thermal sensitivity or thermal coefficient was determined by dividing the maximum increase or decrease in discharge rate by the maximum change in scrotal temperature. Units that increased their firing rate with a rise of scrotal temperature and had a positive thermal coefficient greater than 0.8 impulses sec °C to changes in scrotal temperature were considered as warm-responsive. Units that increased their firing rate with a fall of scrotal temperature and had a negative thermal coefficient greater than 0.5 impulses·sec^{-1}·°C^{-1} to changes in scrotal temperature were considered as cold-responsive[11]. Units that displayed no change in firing rate with changes in scrotal temperature were classified as thermally unresponsive. At the end of

Effects of tail pinch on striatal units classified as cold-responsive, warm-responsive, or thermally unresponsive

No. of units	Noxious stimuli produced by pinching the tail with forceps
24	Cold-responsive unit response
13	Facilitated
11	Inhibited
0	None
33	Warm-responsive unit response
22	Inhibited
8	None
3	Facilitated
20	Thermally unresponsive unit response
12	None
5	Inhibited
3	Facilitated

each experiment, the vertical location of the micropipette was recorded and 25 μA of negative current was passed through the micropipette for 10 min to deposit fast green dye at the site[12]. The locations of the fast green spots were used to verify the location of the recording sites.

The table shows that the proportions of cold-responsive, warm-responsive and thermally unresponsive units were 31.2%, 42.9% and 25.9%, respectively, of the total units recorded in the striatum. Of the 77 units tested, only 2 or 3 were influenced by mechanical (such as light touch or pressure) stimulation of the scrotum or the tail. In 24 out of 77 units, the thermal coefficients were between −0.6 and −1.4 impulses·sec^{-1}·°C^{-1}. They were classified as cold-responsive. Figure 1 demonstrates the discharge rate of a cold-responsive units as influenced by variations in the scrotal temperature. The unit decreased or increased its firing rate in response to the rise or fall of scrotal temperature. The unit was actually more sensitive to decreases in scrotal temperature. 14 units out of the 24 cold-responsive units behaved in this way. The remaining[10] cold-responsive units behaved in a different way; they were thermally unresponsive over part of the temperature tested. The activity of a unit in this category increased in response to a fall of scrotal temperature, but remained unchanged as the scrotal temperature rose.

On the other hand, in 33 out of 77 units, the calculated thermal coefficients were between 0.8 and 1.6 impulses·sec^{-1}·°C^{-1}. They were classified as warm-responsive. An example of a neuron in this category is shown in figure 2. It increased or decreased its firing rate in response to the rise or fall of scrotal temperature. Again, it was found that the unit was more sensitive to decreases in scrotal temperature. 22 warm-responsive units behaved in this way. However, the remaining 11 warm-responsive units were thermally unresponsive over part of the scrotal temperature range tested. The activity of a unit in this category increased in response to a rise of scrotal temperature, but remained unchanged as the scrotal temperature fell. Furthermore, a typical thermally unresponsive neuron is shown in figure 3. The unit responded neither to an increase nor to a decrease of scrotal temperature. The average spontaneous firing rate of the units tested in the present study was 12.1 ± 9.8 (SD) impulses·sec^{-1}. There was no correlation between the cells' responsiveness and their spontaneous firing rate.

It can be seen from both figures 1 and 2 that changes in scrotal temperature caused no dynamic response. A step change in discharge rate of a given unit occurred when the scrotal temperature reached a critical level. Neuronal discharge maintained a fairly constant rate of firing at a given scrotal temperature and showed no sign of adaptation. It was also found that the proportion of the thermally responsive units responding to noxious stimulation was very high, from 76% of the total warm-responsive units to 100% of the total cold-responsive units (table). However, the majority (60%) of the total population of the thermally unresponsive units recorded in the striatum showed no sensitivity in response to noxious stimulation. Of 24 cold-responsive units, 13 units were facilitated by noxious stimulation. An example of a neuron in this category is shown in figure 1. The remainder[11] were depressed by noxious stimulation. Of 33 warm-responsive units recorded in the striatum, 22 units were depressed by noxious stimulation. An example of a neuron in this category is shown in figure 2. In contrast, 3 out of 33 warm-responsive units behaved in a different way; each unit was excited by noxious stimulation. The remaining 8 warm-responsive units showed no response to noxious stimulation. On the other hand, 25% of the total thermally unresponsive units showed an inhibition in response to noxious stimulation. An example of a neuron in this category is shown in figure 3. The other 15% of the total thermally unresponsive units behaved in a different way.

It has been shown that the scrotal skin in rats contains both 'cold' and 'warm' receptors[13]. It has also been shown that neuronal responses to changes in scrotal temperature were observed in the dorsal horn of the spinal cord[10], in the ventrobasal complex of the thalamus[14], in the hypothalamus[15], and in the somatosensory cortex in the rat[16]. Our experiments demonstrated that the majority (74.1%) of the total population of the striatal neurons tested were influenced by thermal stimulation of scrotal skin. In addition, the majority (74%) of the neurons in the striatum tested were affected by noxious stimulation of the tail. The data demonstrate that striatal neurons receive both thermal and nociceptive afferents arising from the rat's skin. The results also show that there exists a high correlation between the thermal sensitivity and the nociceptive sensitivity in the striatal neurons. All the cold-responsive units and 76% of the total warm-responsive units recorded in the striatal area were affected by noxious stimulation. Therefore, the contention that striatal neurons are involved in central control of thermoregulation[4,5] and the nociceptive reflex[6,7] is supported by the present results.

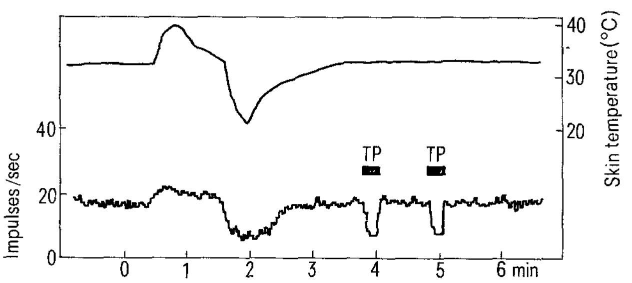

Figure 2. An example of a warm-responsive unit recorded in the striatal region. The firing rate of the neuron increased with scrotal warming. The neuron showed an inhibition in response to tail pinch (TP).

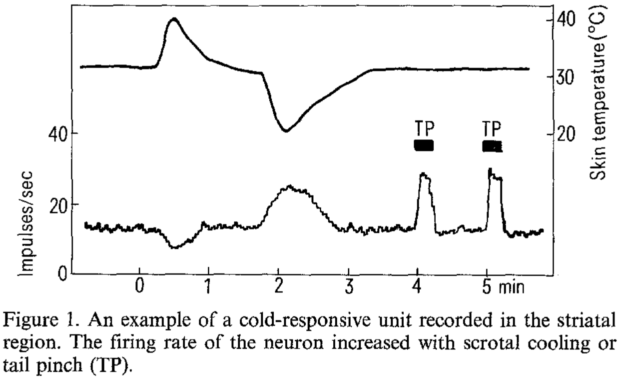

Figure 1. An example of a cold-responsive unit recorded in the striatal region. The firing rate of the neuron increased with scrotal cooling or tail pinch (TP).

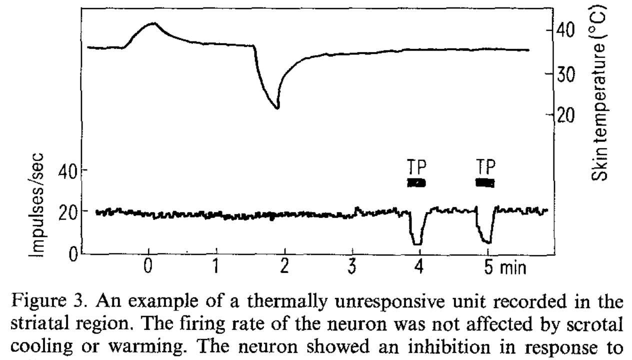

Figure 3. An example of a thermally unresponsive unit recorded in the striatal region. The firing rate of the neuron was not affected by scrotal cooling or warming. The neuron showed an inhibition in response to tail pinch (TP).

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2 Fonnum, F., and Walaas, I., in: The Neostriatum, p.53. Eds I. Divac and R.G.E. Oberg. Pergamon Press, Oxford 1979.
3 DeLong, M.R., and Georgopoulos, A.P., in: Advances in Neurology, vol.23, p.137. Eds T.N. Chase, N.S. Wexler and A. Barbeau. Raven Press, New York 1979.
4 Lin, M.T., Chandra, A., Tsay, B.L., and Chern, Y.F., Am. J. Physiol. *242* (1982) R471.
5 Ho, L.T., and Lin, M.T., Metabolism *31* (1982) 791.
6 Lin, M.T., Wu, J.J., Chandra, A., and Tsay, B.L., J. neural Transm. *51* (1981) 213.
7 Lin, M.T., Wu, J.J., and Tsay, B.L., Expl Neurol. *83* (1984) 71.
8 König, J.F.R., and Klippel, R.A., The Rat Brain: A Stereotaxic Atlas of the Forebrain and Lower Parts of the Brain Stem. Williams and Wilkins, Baltimore 1963.
9 Lin, M.T., and Simon, E., J. Physiol. *322* (1982) 127.
10 Hellon, R.F., and Misra, N.K., J. Physiol. *232* (1972) 375.
11 Kelso, S.R., Perlmutter, W.N., and Boulant, J.A., Am. J. Physiol. *242* (1982) R77.
12 Hosford, D., and Haigler, H.J.J., J. Pharmac. exp. Ther. *213* (1980) 355.
13 Iggo, A.J., J. Physiol. *200* (1969) 403.
14 Hellon, R.F., and Misra, N.K., J. Physiol. *232* (1973) 389.
15 Nakayama, T., Ishikawa, Y., and Tsutani, T., Pflügers Arch. *380* (1979) 59.
16 Hellon, R.F., Misra, N.K., and Provins, K.A., J. Physiol. *232* (1973) 401.

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Short-distance homing in a small mammal: the role of exteroceptive cues and path integration

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Summary. When hoarding food under IR light, the golden hamster returns to its nest by path integration after an active outward journey, and it is capable of compensating the angular component of a passive outward journey independently of auditory, olfactory, tactile and geomagnetic cues. If, however, peripheral visual cues are available, they predominate over information which is gained during the active or passive outward journey. Further experiments show the limitations of homing by path integration, which is open to cumulative errors and therefore needs to be complemented by other categories of information.
Key words. Hamster, golden; *Mesocricetus auratus*; homing, short distance; exteroceptive cues; path integration.

The question to what extent spatial orientation can occur without being controlled by exteroceptive information has preoccupied comparative psychologists since Watson's pioneering work[2] and has, more recently, been reformulated from an ethological and biocybernetic point of view[3-5]. Experimental evidence that this may be the case in higher vertebrates has to be gained either through the attempt to eliminate all possible directional cues from the environment, or through the more satisfactory demonstration that such cues can, on logical grounds, not explain the observed behavior.

Within the limited space of an experimental arena, golden hamsters (*Mesocricetus auratus* W.) hoard food by carrying it directly to their peripherally located nest site. As shown by previous experiments[6], some animals maintain significantly orientated homing itineraries in conditions which simulate long distance homing by a passive outward journey combined with the simultaneous elimination of visual, auditory, olfactory and tactile cues. This unexpected result opened up the question as to whether the animals orientate menotactically with respect to a still unknown external frame of reference, or whether they home by path integration. In the second case, their behavior would, most probably, be controlled by vestibular information[7,8] and could therefore be interpreted as inertial navigation[9,10].

The subjects, mostly adult females, remain in their own arena (∅ = 2.20 m), which is located in a cellar with heavy walls and no windows, throughout the experimental period. They are provided with a nest box which is fixed to the outside of the arena's peripheral wall. 12 doors are set in the base of this wall at an angular distance of 30° from each other; all, except one, which gives access to the nest box, are permanently closed. In each trial, a pile of hazelnuts is placed at the centre of the arena; the subject, having filled its cheek-pouches, returns to the periphery of the arena in search of the nest entrance. The animals's return path is coded in terms of its location at the moment it crosses each of six concentric and equidistant circles, within any of the 12 sectors of 30°, which subdivide the arena's floor. The most peripheral of these circles is located at a distance of 15 cm from the sidewall of the arena and delimits a 'peripheral zone'. In trials with an active outward journey, the animal walks from its nest exit (which leads into the arena) to the centre of the arena, following a bait which the experimenter moves in front of its nose. In trials with a passive outward journey, the animal goes directly from its nest exit into a transportation box (16 × 18 × 25 cm), which is then moved to the centre of the arena. The animal is released from the box when the latter has been rotated in such a way that the subject enters the central zone of the arena with its head pointing either towards the nest entrance or ±90° or 180° away from it.

The following procedures were used to eliminate or mask directional cues from the environment. Visual cues: Unless mentioned differently, all trials take place under IR light (peak emission at 940 nm, bandwidth = 45 nm[11]). Auditory cues: 'pink noise' (bandwidth = 45–20,000 Hz) is emitted from four (mobile) loudspeakers; at the same time, the sound-reflecting properties of the experimental room are altered at regular intervals by the displacement of panels covered with vetroflex and strongly-absorbing acoustical foam along the walls. Olfactory and tactile cues (on the floor of the arena): at regular intervals, a thick substrate of sawdust which covers the arena's floor is stirred thoroughly and then flattened out again. All kinds of cues within the arena: In most experiments with a passive outward journey, the technical procedures involved in 50% of the trials included the rotation of the arena by ±90° or 180° after the animal had left the nest; during the rotation of the arena, the subject was kept in the transportation box which was lifted above the arena's floor. If the animal continues to return towards the usual, i.e. 0°, location of the nestbox in