contrast to the results obtained by Siegel et al.[16] in the genus *Nicotiana*, where diploid species possess about twice the rDNA percentage with respect to tetraploid species, so that the number of 80S rRNA cistrons is roughly the same in both. On the other hand, Siegel's data have not been confirmed by Cullis in *Nicotiana*[17] and in *Datura*[18] and by Maggini et al. in *Scilla autumnalis* and *Urginea maritima*[19].

Many factors, including rRNA cistrons, influence the level of protein in the seed. We thought that the ribosomal cistron number might correlate with the total protein content of the seed. This is not the case in *Triticum* species. In fact in the diploid and tetraploid species studied there is no correlation between rDNA percentage and seed protein content. In this context Phillips[10] hypothesized that in *Zea*

mays only a few rRNA genes are transcriptionally active, while the bulk of rRNA genes are useful only at certain developmental stages or under stress conditions. Since no differences in the DNA content per nucleus were found among 25 varieties of common wheat *(T. aestivum)* by Nishikawa and Furuta[20], we feel that an intraspecific stability of DNA amount per genome exists in each of the 4 *Triticum* species studied. As a striking example, assuming 24.2 pg as the DNA content per 2C nucleus in *T. durum*[21] and 2×10^6 daltons as the molecular weight of the rRNA, we calculated rRNA gene numbers of 5500 and 10,400 respectively in *T. durum* cv. Valnova and Ranger, and the seed protein contents were 16.29% and 16.84% respectively. Phillips'[10] hypothesis could partly explain these results, but the question remains open.

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The orientation of the golden hamster to its nest-site after the elimination of various sensory cues

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Summary. Golden hamsters hoard food by carrying it back to their nest-site along a fairly direct path. 7 out of 12 animals continued to orientate in this way after passive transportation to the food source and the simultaneous elimination of visual, olfactory and acoustical cues. Experiments in which the hamsters tried to reach their nest-box from an unfamiliar place suggest that they orientate in a given direction with respect to a 'compass', the nature of which has still to be determined.

Preliminary observations and experiments have shown that within a familiar environment the golden hamster (*Mesocricetus auratus* Waterhouse) transports food to the habitual location of its nest-box by a fairly direct route, and that the animal maintains this orientation in spite of the elimination of various cues. The following 2 questions are therefore examined in this paper: a) Does the animal find the direct way back to its nest-site after being carried passively to the food source, and when visual, olfactory and acoustical cues have been simultaneously eliminated? b) Is the animal's direct orientation to the nest-site limited to the space it lives in, or can it 'home' from unfamiliar places? According to Bovet[2] this is the case for myomorph rodents which are released outside their home range; other authors, on the contrary, assume that there is as yet no convincing evidence for true navigation in rodents (see summary of literature in Joslin[3]).

All experiments took place under IR light in a cellar with thick external walls, double doors and no windows. The animals live under an artificial light dark cycle (dark: 18.00–06.00 h) and they are tested between 20.00 and 23.00 h, when the building is empty. Each individual occupies on its own a turnable arena ($\varnothing = 2.20$ m), where it

is introduced a few days before the beginning of the experiments and where it remains[4] and moves freely throughout the experimental period. The arena's peripheral wall is made out of aluminium and is 50 cm high. 12 circular doors, hinged at the top, are set in the base of this wall at an angular distance of 30° from each other; all of them are permanently closed, except for one, through which the hamster can move freely in and out of a nest-box which is fixed to the outer side of the arena.

At the beginning of each trial, the animal is taken into a black box as soon as it leaves its nest-box; using a dim light, it is then deposited at the edge of a food bowl located in the centre of the arena, the orientation of the animal's head as well as the experimenter's own position being systematically varied from one trial to the next. When it has filled its pouches, the animal is allowed to go back to the arena's periphery, where it finds the nest entrance either directly or by searching movements along the circular enclosure.

The following procedures are used to eliminate various sensory cues simultaneously.

1) Optical cues. These cues are always eliminated, as the animals are filmed through an IR video-camera which is located above the centre of the arena and monitored from

an adjacent room. Filming occurs under an IR projector suspended 2.30 m above the arena's floor. The projector contains a halogen tube which is supplied by a potentiometer set at 40 W. Light is diffused through a Schott filter (16.3 × 13.5 cm) which transmits 50% light at 1000 nm, and 10^{-3}% light at 800 nm. Previous behavioural and electrophysiological experiments have shown that the hamster's visual responsiveness to red and near IR wavelengths stops at 740 nm[5].

2) Acoustical cues. To mask frequent noises stemming from pumps, pipes etc. within the building, 4 loudspeakers, which are supplied by 4 independent noise generators, diffuse pink noise (bandwith = 45–20,000 Hz) against the walls of the experimental room throughout the experimental trials; the position of these loudspeakers is changed from one experiment to the other. Control measurements within a bandwidth of 63–8000 Hz showed that the background noise is covered within these limits; they further suggested that the intensity of background noise is well below that of the pink noise at higher frequencies, whereas this may not be the case at frequencies below 63 Hz.

3) Olfactory cues. The arena's floor is covered with a thick layer of sawdust, which is thoroughly stirred before the start of the trial. Furthermore, as soon as the hamster has left its nest and entered the transportation box, the arena is turned (clockwise or anti-clockwise) by 90, 135 or 180°, the nest-box being displaced a corresponding amount from its usual position with respect to compass directions.

In order to analyze the animal's itinerary from the centre of the arena to its periphery, a transparent drawing is superimposed on the video-monitor; it allows the experimenter a) to subdivide the arena's floor into 12 sectors, each sector corresponding to an arc of 30°, and b) to superimpose on it 6 equidistant, concentric circles. In this way it is possible to determine in which of the 30° sectors the animal transgresses each of the 6 circles. The standard deviation between the points of transgression of the 6 circles is computed in order to describe the degree of rectilinearity of each run. To calculate the mean vector[6] of a series of itineraries followed by 1 animal, only the point of transgression of the most peripheral circle, which is located at a distance of 15 cm from the arena's peripheral wall, is taken into account; in fact hamsters sometimes reorientate on their way out to the periphery, and thus show their final orientation most celarly just before reaching the latter. The length of time the animal takes to go from the centre of the arena to the most peripheral circle and to the entrance of the nest-box is also measured.

A) A first series of experiments included 5 trials during each experimental session, which took place during 8–12 consecutive nights. The first 4 trials, called 'reference trials', were performed without optical cues, after passive transportation to the centre of the arena. The 5th trial, called 'critical trial', was performed with additional elimination of olfactory cues and masking of acoustic ones. Out of 12 animals which oriented significantly towards the nestbox during reference trials, 7 maintained a correct orientation during critical trials, i.e. they went in the compass direction where the nest-box was located before the arena was rotated (figure 1). The 5 remaining animals orientated in an erratic way during the critical trials, without showing any directional trend with respect to the usual location of the nest-box or to its new location after rotation of the arena.

The 7 animals which went in the direction of the usual location of the nest-box throughout the experiment took at an average 3.1 sec to go from the centre of the arena to the zone located at a distance of 15 cm from its periphery during the reference trials, and 3.2 sec during the critical trials. Various statistical controls using the Wilcoxon matched-pairs signed-rank test[7] showed that the characteristics of critical runs did not in general vary in quality from those of the reference trials; only 1 test animal showed a significantly (p < 0.02) smaller standard deviation between the points of transgression of the 6 circles (see above) in critical trials and thus increased the rectilinearity of its itineraries under the increased deprivation of sensory cues.

B) The next step in this research was to examine whether the hamsters orientate systematically with respect to the habitual location of their nest-box when they hoard food in a new space, where they have never been before. To test this question the animals were at first allowed to hoard food in their own arena A during 4 reference trials; these trials took place under the simultaneous elimination of visual, olfactory (stirring of sawdust only) and acoustical cues, and the subjects were shifted passively to the food bowl located at the centre of the arena. In a 5th trial, which took place immediately after the 4th reference trial and which was run under the same conditions, the hamsters were deposited in the centre of an unfamiliar, adjacent arena B which was located on the same side as the nest-box of arena A (figure 2). To avoid the animals' exploring the new environment instead of hoarding the available food there, the floor of arena B had been covered with some of the sawdust previously contained in arena A and therefore had a familiar odour.
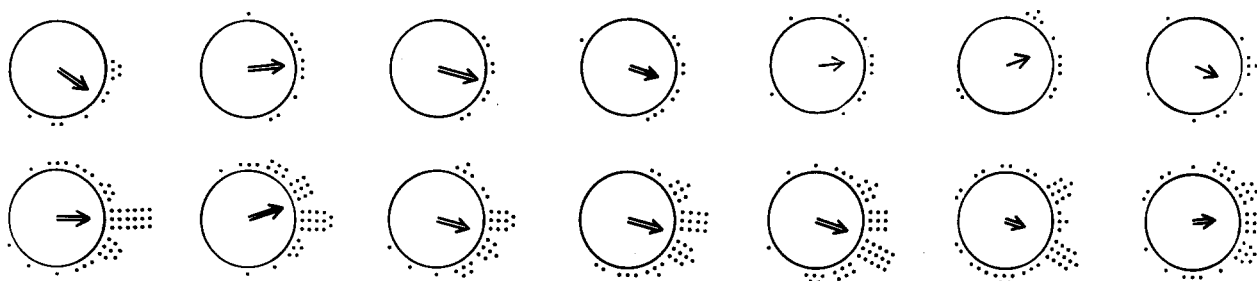
Fig. 1. The orientation of 7 animals towards the usual location of the nest-box after passive transportation to the hoarding place and the elimination of various sensory cues. During 4 reference trials using IR light, the animals are released at the centre of the arena, where they find food. During a 5th, critical trial, olfactory (stirring of sawdust, rotation of arena) and acoustical (pink noise) cues are also eliminated. The diagrams represent the floor of the arena; the normal location of the nest-box is always shown to the right. Each diagram on the upper row refers to the reference trials of a single animal; the diagrams on the lower row refer to the performance of the same animals during the critical trial. Each dot indicates in which sector corresponding to an arc of 30° the animal was when it reached a zone located at a distance of 15 cm from the arena's periphery. The arrows indicate the mean vector of the animals' orientation during consecutive trials; their length is proportional to the consistency of orientation of particular trials around the mean direction (maximal length = 1, i.e. length of the radius). A double arrow indicates that the animal was orientated at a significance level of 1%; a simple arrow indicates that the 5% limit was reached (Rayleigh test[6]).
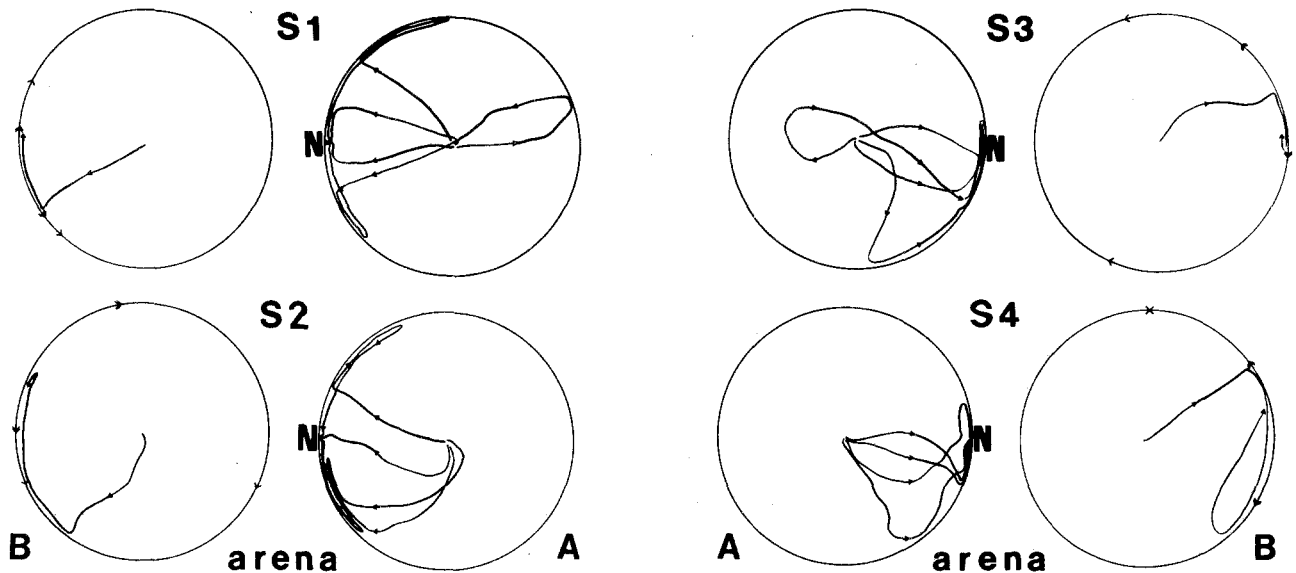
Fig.2.The orientation of 4 animals (SI-S4) with respect to their nest-box (N) within an unfamiliar environment. Each hamster lives in arena A and has never been in an adjacent arena B. In 4 reference trials, the animals are deposited at the centre of their own arena A from where they hoard food. In a 5th trial, the animals are deposited at the edge of a food bowl located at the centre of arena B. During all trials, optical, olfactory and acoustical cues are eliminated. The diagrams represent the animals' itinerary to the periphery of the arena during the reference trials 1-4 in their home arena A and during trial 5 in the unfamiliar arena B. On the diagrams representing arena B, 2 thick arrows delimit the zone of the arena's periphery where the subjects started to search the entrance of the nestbox by back and forth movements during the first 15 sec, and 2 thin arrows delimit the complete zone which the animals explored during the 90 sec they were left in arena B.

Under these conditions, 3 types of reactions could be expected to occur in the unfamiliar arena B: 1. The animal behaves randomly. 2. It orientates in the same compass direction as it did before in its own arena A, thus maintaining a given direction with respect to an unknown external cue which acts from outside both arenas. 3. It orientates in a compass direction which is the opposite of that in arena A, and thus goes back towards the actual location of its nest-box; as the animal could not be guided by any stimulus originating from the latter, this reaction would seem to imply some principle of inertial navigation[8].

7 hamsters were tested according to this technique; they all reacted according to the same principle, which is exemplified in figure 2 by the results of the first 4 experiments of this type. Obviously, the animals orientated in the unfamiliar arena along the same rough compass direction as they did in the familiar one, both with respect to their orientation from the centre to the periphery of the arena and to the peripheral zone where they started to search for the entrance of the nest-box in the unfamiliar space of arena B.

On the basis of this result the correct orientation towards the usual location of the nest-box which certain animals maintained in experiment A after elimination of various sensory cues may be interpreted as 'compass orientation', the physical nature of the compass having still to be determined. Experiments which analyze the influence of particular components of the earth's magnetic field[9] are in progress, and it is planned to test the possible role played by sounds[10] beyond the band-width of the pink noise which has so far been used to mask current background noises. In a complementary line of research, specific categories of external[11,12] as well as idiothetic[13] information are given to the animals in order to see what kind of cues they use spontaneously for their orientation when they are presented with them rather than being deprived of them[14]. It is hoped that the use of procedures which imply a limited, yet

physically controllable space will help us to gain a better understanding of how certain rodents orientate in their natural environment.

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