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Depth perception by means of ambient sounds in a small mammal[1]

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Summary. Golden hamsters placed on a jumping stand from which they can descend onto a shallow or deep landing platform prefer to descend on to the shallow platform, even when tested under IR-light without tactile cues. This preference disappears for subjects with plugged ears. The simultaneous recording of the animal's behaviour and possible emission of ultrasound as well as experiments in which the external acoustical conditions or the sound-reflecting properties of the jumping apparatus were altered suggest that the animals use certain parameters of the ambient sound field for depth perception.

Depth perception in mammals has mainly been studied with respect to vision (for a summary of the literature, see Thinus-Blanc[2]). The perception of space, however, may involve sensory modalities which vary according to the animal's sensory equipment and way of life in a given environment. Furthermore, a given species may use different categories of external cues in different test situations.

Golden hamsters *(Mesocricetus auratus W.)* are active at night and probably spend most of their time underground, like other burrow-dwelling rodents. Extensive experiments with a visual cliff have shown that these animals can use visual criteria for depth perception, but that they are more influenced by tactile stimuli if both categories of cues are presented in a conflicting way[3]. Similarly, the behavior of hamsters tested on a real cliff, where the animal cannot use tactile cues, reveals that the estimate of depth is more accurate under white light, yet is by no means abolished in complete darkness[4]. Thus, depth perception seems to occur in this species when both visual and tactile stimuli are eliminated. The aim of this research was, therefore, to examine the role of auditory cues in the above-mentioned situation. If these cues should prove to provide the animals with the relevant information, further experiments should establish a) whether the subjects themselves produce sounds which are reflected by nearby objects (active echolocation), or b) whether they perceive certain features of their acoustical environment which translate the interaction between external sound waves and objects. These features may correspond to patterns of sound reflection, absorption and diffraction.

In most experiments, golden hamsters of both sexes, aged 3-20 months, were tested on the jumping stand represented in figure 1a, which was located in a room A, on the 1st floor of a city building. Each subject was placed by an experimenter on the center of the start platform, its head facing one of the 2 plexiglas walls. To place the animal correctly, the experimenter very briefly used a weak electric torch. The animal was then able to leave the start platform by choosing one of the 2 landing platforms, located at a distance of 20 cm and 105 cm from the start platform. The cliff, 20 cm deep on the shallow side of the apparatus, did not allow the subjects to obtain tactile information through the vibrissae during frequent head dippings which occured at the edge of the start platform. To exclude visual information, the animals were always video-filmed under IR-light; the IR-projector containted a halogene tube (supplied by ≤ 100 W) and a Shottfilter which transmitted 50% light at 850 nm, and 10^{-3}% light at 780 nm. According to previous behavioral and electrophysiological experiments, the hamster's visual responsiveness to red and near-IR wavelengths stops at 740 nm[5]. Precautions were taken to eliminate olfactory cues which might have been left on the apparatus by previously tested subjects: after each experiment, the start- and landing platforms were thoroughly cleaned with alcohol and water. To neutralize possible side preferences, the heights of the 2 landing platforms were exchanged after every 2nd experiment. Animals which did not leave the start platform after 20 min, which left the platform through accidentally falling off, or before they had explored both sides of the cliff with head dippings, were excluded. 'Naive' animals, which had never been tested on the jumping stand, were given the opportunity to explore the latter approximately 5 h before the test, with both landing platforms being raised to a distance of 5 cm below the start platform.

The animals were observed on a video-monitor located in an adjacent room. Their behaviour was recorded in terms of 1. the choice of descending either on the near or distant landing platform, 2. the latency of this choice, and 3. the number of head dippings (animal holding itself with forepaws at the edge of the start platform and lowering its head beneath the level of the platform either very briefly or with superimposed horizontal exploratory movements) on either side of the start platform prior to leaving it.

In previous experiments, the subjects increased the latency with which they left a circular jumping platform as a function of the latter's height above floor level[4]. It was, therefore, to be expected that in the choice situation of the present experiment, the hamsters would prefer to descend on the shallow, rather than on the deep side of the jumping apparatus. Figure 2a shows that this was indeed the case, both for naive subjects tested for the first time and for experienced animals which had already been used in similar experiments.

The next step in this research was to eliminate the use of hearing, in addition to vision and touch, in naive animals. Approximately 21 h prior to testing the experimental subjects' external auditory canal was filled (under anesthesia) with dental cement (Dropsin). Immediately before they were released on the jumping stand, the reaction of these subjects to a repeatedly-produced, very loud sound with a broad frequency range was carefully observed under IR-light in order to eliminate animals whose hearing did not seem sufficiently impaired. Control subjects were also anesthesized, but their ears remained untouched. The behaviour of the animals on the jumping stand showed that while the controls continued to choose the closer landing platform significantly more often, the experimental subjects tended to leave the start platform sooner and without showing any side preference (fig. 2b). (During the experiments, these animals did not show any behaviour which might have suggested that they were disturbed by the earplugs. In other situations, they scratched their ears frequently and in general succeeded in extracting the dental cement plugs in one piece within 2 or 3 days after their insertion.)

If acoustical cues represent the main criteria for depth perception in our experimental situation, the use of these cues suggest the following alternative explanations. Our subjects either produce exploratory sounds in order to analyze certain features of their spatial environment by acoustical feedback effects, or they use for this purpose external sounds which are reflected (and modified in various other ways) by surrounding objects and surfaces. This alternative was approached by the following 3 procedures: a) the simultaneous registration of the animal's behavior on a real cliff and of ultrasounds which may be emitted during the test situation; b) the repetition of the initial experiments in a quiet room; c) the variation of certain parameters of the jumping stand which may influence the way in which actively produced as well as ambient auditory cues are received by the subject.

a) Eight experienced hamsters were tested in a laboratory for building acoustics (room B). Each subject was placed on a small circular jumping stand, elevated 62.5 cm above the floor. On the basis of preliminary results, 2 microphones situated beneath the stand received noise signals in the bandwidth of 22–44 kHz (oc. 31.5 kHz). These signals were transduced via a spectrometer to a level recorder and an oscilloscope. The recording technique permitted us to view simultaneously the animal's behaviour under IR-light and the waveform of the US-signals on the oscilloscope screen. 7 of the 8 subjects jumped to the floor, and all subjects produced US-signals in the above-mentioned frequency range. Among the 104 US-signals which were recorded, 75% accompanied head dippings or scratching movements on the stand. With respect to their waveform, duration and temporal recurrence, these signals corresponded neither to US-emissions which male and female hamsters use for mutual communication[6] nor to the often paired and rhythmically recurring US-pulses which are used by 'simpler echolocators'[7]. In general, the emitted US-signals seemed not to be produced vocally; rather, they could be interpreted as frictions of the animal's paws and claws on the jumping platform, which can be expected to occur during head dippings as well as during obvious scratching movements. As shown by Riley and Rosenzweig[8], the possible use of the US-components of scratching as actively produced echolocatory cues must not be overlooked.

b) The experiments with our normal jumping stand were repeated in a room located in a cellar, which had no windows (room C). Acoustical measurements within the bandwidth of from 12.5 Hz to 80 kHz showed that the intensity of the loudest sound impulses recorded in the cellar (C) was consistently ≥ 17 db lower than the response threshold of single units in the hamster's cochlear nerve[9]. In the normal experimental room (A), on the contrary, the energy level of frequently occurring, short sound impulses (≤ 35 msec duration) was sufficiently high to stimulate auditory units, particularly within a frequency band of 1000–2000 Hz (in both rooms A and C, no sounds of an energy level superior to 0 db could be detected above the frequency of 8000 Hz). Graph 2c shows that in the cellar, experienced as well as naive subjects still have a slight preference for the shallow side of the jumping apparatus, but this preference is by no means significant. It seems, therefore, that in the cellar, the reduction of the intensity of sound impulses in the above-mentioned frequency band reduces the subjects' capacity to distinguish between the deep and the shallow side of the

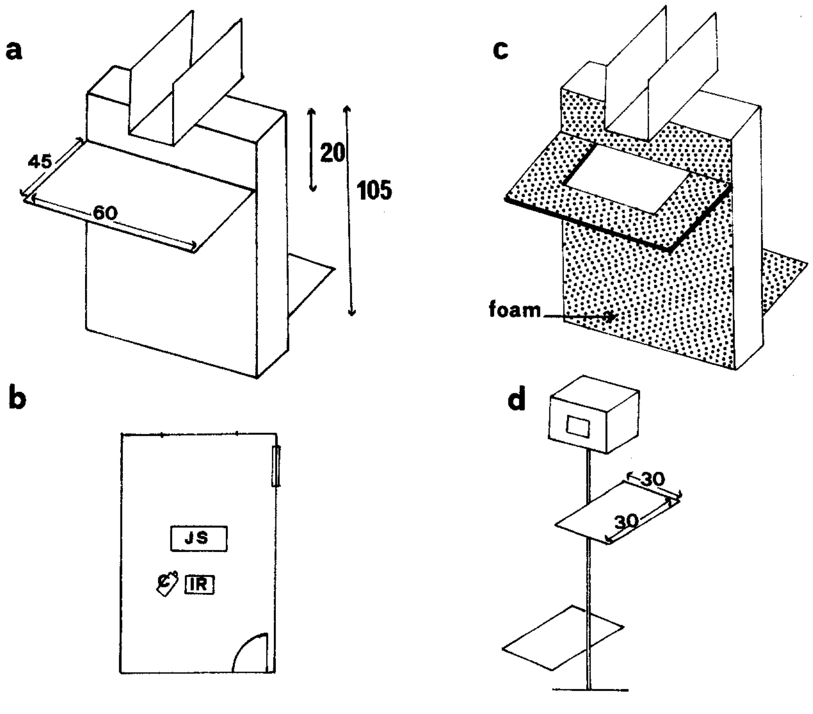

Figure 1. Test apparatus. *a* Normal jumping stand with broad central base (conglomerate), start platform (PVC base and plexiglas walls) and the 2 landing platforms (wood covered with PVC and plastic sheet) *b* Normal experimental room with jumping stand (JS), video camera (C) and IR projector (IR). *c* Normal jumping stand covered with acoustic foam. *d* Jumping stand of reduced dimensions; the start platform is made of plexiglas, the landing platform and central axis are metal. The numbers on graphs *a* and *b* correspond to cm.

jumping stand. This supports the hypothesis that ambient noises can provide the animal with important cues for depth perception. On the other hand, the animals' slight preference for the shallow side might also imply the use of the above-mentioned, self produced contact noises.

c) Two further experiments were carried out in room A to analyse to what extent the sound-reflectory properties of the jumping stand influence the animals' choice behavior. The landing platforms of the usual jumping stand (fig. 1a) represented an efficient sound mirror with respect to its dimensions and (hard) surface. In a 1st experiment, the animals were tested on a jumping apparatus of reduced size (fig. 1d); they showed no capacity for choosing the shallow side of the cliff on this smaller jumping stand (fig. 2d). A 2nd experiment implied changes in the surface properties of the usual jumping stand, which was covered with acoustic foam (fig. 1c). Figure 2e shows that under these conditions, the subjects again lost their preference for the shallow landing side of the normal apparatus, their behaviour being similar to that observed on the new jumping stand of reduced dimensions.

It appears, therefore, that the animals can choose the shallow landing side by exclusively acoustical means only when the pattern of sound reflection on both sides of the cliff is sufficiently distinctive. In this respect, the dimensions of the sound-reflecting area of the shallow landing platform itself, and in relation to the wavelength of the ambient sound impulses, are of primary importance, as are the spatial relationships between the location of the sound source, the reflecting surface or object, and the receiver[10]. As mentioned above, the normal experimental room (A) differed from the cellar (C) (where no side preference occurred) by the presence of sound impulses which were within the response range of the subjects' auditory system; some of these impulses may well have corresponded to the upper frequency range of impact noises which originated on the supper floor and, therefore, were transmitted through the ceiling. On the other hand, we wish to emphasize that the subjects may also have perceived very global differences in the sound field, which are not only related to the reflection of sound impulses.

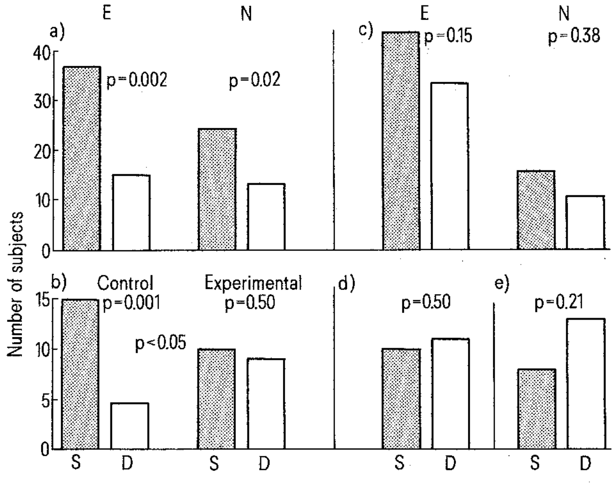

Figure 2. Choice frequency of the 2 landing platforms in various experimental conditions. The histograms represent the number of subjects which choose the shallow (S) and deep (D) side of the jumping stand. *a* Initial experiments on the normal jumping stand with E (experienced; n = 52) and N (naive; n = 40) subjects. *b* Experiments with subjects having plugged ears, conducted on normal jumping stand. Control subjects (n = 17); experimental subjects (n = 19). The differnce between the choice behavior of the 2 groups is significant at the 5% level (χ^2-test). *c* Experiments on normal jumping stand in a quiet environment, with E (n = 78) and N (n = 21) subjects. *d* Experiments with jumping stand of reduced size (n = 21). *e* Experiments with normal jumping stand, the sound-reflecting properties of which have been rendered similar to those of the smaller jumping stand (n = 21). The probability values above each pair of histograms correspond to the probability of the difference between the choice frequency of the landing platforms (binomial test).

That the subjects always perceived some difference in the acoustical information on both sides of the jumping stands is suggested by differences in the amount of head dippings. Unless their ears were plugged, the subjects that chose to descend on the shallow platform always performed significantly (Wilcoxon test) more head dippings on the shallow side than on the deep side of the cliff. With the exception of the experienced subjects which are described by graph 2c, the animals which chose the deep landing side, on the contrary, did not show significantly more head dippings on this side of the start platform prior to leaving it. Head dippings, therefore, may not only be interpreted as preparatory or intention movements for leaving the start platform on the corresponding side, but also as an exploratory activity that provides the animals with pertinent acoustical information. (The mean latencies with which the subjects of all experimental groups left the start platform varied from 220–547 sec, and showed no systematic tendency with respect to the pertinent parameters of the experiments. However, naive subjects (a) and animals with plugged ears (b) left the start platform sooner than experienced subjects (a) and animals with intact hearing (b).

Our findings are in agreement with the observations of other investigators that golden hamsters can use acoustical cues for depth perception[11], but they do not echolocate by means of vocal sound production[12], as is the case for shrews[13,14] and other vertebrates which do not belong to the order Microchiroptera[15,16]. That a given species may use external noises (if available) as well as actively produced nonvocal sounds to locate a landing platform in a test situation similar to the present experiments has recently been demonstrated in woodrats[17]. As indicated by the authors, the precise characteristics of the external sounds used for space perception are as yet unknown.

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