Perceptual and Motor Skills, 1984, 58, 291-298.

SENSORY MODALITIES IN DEPTH PERCEPTION BY GOLDEN HAMSTERS[1]

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Summary.—Golden hamsters are able to detect differences in the height of a platform from which they jump, as measured by their increasing latencies prior to jumping from increased elevations. This ability is very effective when optical information is available, but it is also present when hamsters jump in total darkness. A second experiment shows that, when hamsters are placed on a real physical cliff, they preferentially use tactile information over visual information to guide their choice of the side from which to descend. In a nonvisual setting, tactile stimulation is used in conjunction with other types of cues. Evidence is provided to suggest that these cues are of an acoustical nature.

Perception of space by mammals depends generally on a variety of cues which pertain to different sensory modalities. In animals' natural way of life, one modality typically has gained a functional priority with respect to a given situation which requires a specific adjustment to certain spatial parameters. Under laboratory conditions, therefore, we can examine the type of sensory cues that are used preferentially if different classes of cues are presented in a conflicting manner. Furthermore, we can analyze how the animal changes from one set of cues to another if the presentation of these cues is altered and to what extent certain parameters of space are still perceived through a restricted set of cues which are not necessarily related to the predominant sensory modality.

Golden hamsters (*Mesocricetus auratus* W.) are active at night and, if they have the opportunity, spend much time in their burrows. According to Dieterlen (1959), they use vision mainly to detect moving stimuli and the general features of their environment. However, learning experiments which required the animals to distinguish between different optical configurations showed that they are able to recognize closely-related forms (Knoop, 1954), that they rely strongly on vision in a spatial-orientation task (Brotzler, 1963), and that they can achieve volume discrimination through optical cues (Thinus-Blanc, 1978). Tactile (Schiffman, 1970, 1971) and olfactory (Durup, 1970) cues play a major role within "near space." Finally, hearing is well-developed in rodents, especially in the high-frequency range (Brown, 1971; Sales & Pye, 1974). Golden hamsters communicate over short to moderate distances with

[1]This research was supported by a Janggen-Poehn Stiftung grant and by Fonds National Suisse de la Recherche Scientifique, Grant No. 3.349.74. The authors thank Ms. Peggy Plant for her assistance in preparing the manuscript. Requests for reprints should be sent to J. Vauclair, Centre National de la Recherche Scientifique, Institut de Neurophysiologie et Psychophysiologie (INP 9), 31, Chemin Joseph-Aiguier, 13402 Marseille Cédex 9, France.

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ultrasounds (Floody & Pfaff, 1971), and it has been suggested that they use auditory cues for space perception (Kahman & Osterman, 1951; Vinch & Covalt-Dunning, 1972).

The present paper examined how hamsters perceive depth (or height) in relation to visual and tactile cues. Depth perception in these animals is also discussed with respect to the possible use of olfaction and audition. With respect to audition, golden hamsters continue to show a preference for the shallow side of a real cliff when tested under infra-red light and without the aid of tactile cues. Since this preference is not evidenced in subjects with plugged ears, it has been suggested that depth perception may depend exclusively on auditory cues (Etienne, *et al.*, 1982).

The goals of the present experiment were (a) to provide further evidence that the animals can detect depth without tactile or optical cues in a different experimental setting from that used in the above-mentioned experiments and (b) to describe their behavior in situations where different categories of cues are presented in a conflicting manner. To create this conflict, tactile cues were presented to the animals on the deep side of a real cliff, but these cues were not provided on the side with a shallow landing platform. Furthermore, these conflicting cues were presented under conditions of light and of total darkness to evaluate the relative role of visual and other nonvisual information.

EXPERIMENT I

The ability of the golden hamster to estimate height was investigated by means of a jumping-stand apparatus. By varying the height between the starting platform and a circular open-field onto which the animal could jump, it was possible to measure latencies prior to jumping. It was predicted that an increasing hesitancy to jump at higher elevations would indicate the animal's capacity to perceive differences in height. This capacity was tested under conditions of light and of total darkness.

Method

Subjects.—Twenty male and female golden hamsters (*Mesocricetus auratus* W.) served as subjects. All subjects were housed individually in standard cages and maintained under a 12-hr. light/dark cycle, with no prior opportunity to practice jumping.

Apparatus.—A jumping stand (Cole & Topping, 1969), measuring 31 cm in diameter, was used in the present experiment. A hole in the center of the platform permitted the platform to be raised or lowered along a vertically-mounted steel rod. The two ends of the rod were attached to the ceiling and to the center of a circular open-field (141 cm in diameter with a surrounding wall measuring 30 cm in height.) Both the starting platform and the floor of the open-field were patterned with 3.7 cm wide black-and-white checks. A white blanket surrounded the entire apparatus to provide a homogeneous peripheral visual field. Four 25-W bulbs illuminated the apparatus from the ceiling.

Procedure.—Three heights were chosen: A = 20 cm, B = 62.5 cm, and C = 105 cm. The subjects were divided into two groups. One group (n = 10) jumped from the three levels of the starting platform according to the sequence ABC and the second group (n = 10) jumped according to the sequence BAC. Half the subjects in each group started under the light condition and the other half under the dark condition (total darkness). To familiarize the animals with the starting platform (which was then positioned 5 cm above the floor) and to permit them to explore the open-field for at least 30 sec., the subjects received two preliminary trials prior to initial testing. These trials took place in the morning and were followed by the first test session in the afternoon.

In each test trial, the brief application of a weak electric torch was used to place the subjects individually on the platform, which was already positioned at the predetermined height. The dependent variable, i.e., latency to jump, was measured from this moment to completion of the jump. After jumping, the subjects were allowed to explore the open-field for 30 sec. The second and third test trials of the same test series followed without intertrial interval. After completing three jumps, the subjects were returned to their home cages. Five days later, the subjects were tested again under the second condition with respect to light or dark, in accordance with the same procedure.

To reduce the possibility of vestibular cues, the subjects were submitted to various ascending and descending movements prior to being placed on the starting platform. The metal rod and the platform were cleaned with alcohol after each trial.

Results

In the two experimental sequences and under light and dark conditions, all animals jumped from the starting platform on all trials. As expected, the latencies to jump increased with increased height of the platform in total darkness and in the presence of visual cues (Fig. 1). In addition, for experimental Group BAC, the latencies tended to be longer under conditions of darkness than under the light conditions.

Discussion

The significant increase in latency to jump with increased height of the jumping platform indicates that golden hamsters perceive differences in height or depth. This discrimination is effective when the increments of height are progressive (ABC group). Interestingly, the results show that differences in depth are still perceived without the aid of visual cues. Of course, it is possible that perception of depth can be facilitated by the use of optical informa-

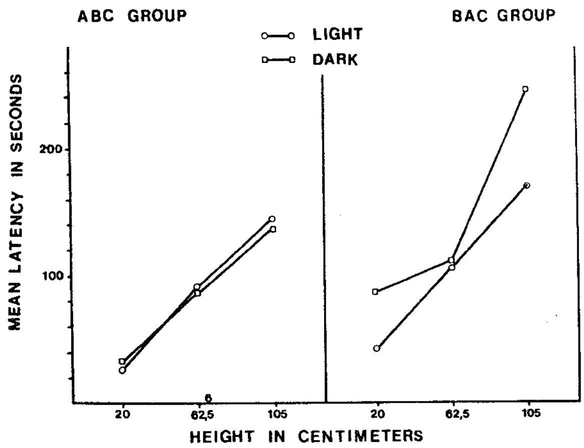

FIG. 1. Group curves ($n = 20$) showing mean latencies (in sec.) as a function of three different heights of the starting platform. (Friedman analysis of variance: ABC light, $p < .001$; ABC dark, $p < .01$; BAC light, $p < .05$; BAC dark, $p < .001$.)

tion, as is evidenced by the reduced latencies of the BAC group under light conditions. Yet, in both experimental sequences, the subjects required more time to jump when the elevation of the platform was increased, even when visual information was not presented. This result confirms our previously published findings (Etienne, *et al.*, 1982), which were obtained on a real cliff with a shallow and a deep landing side. (This apparatus was also used in Exp. II of the present research and is shown in Fig. 2 below.)

Experiment II

The 'classic' visual cliff apparatus (the shallow and deep sides of which are covered with glass) has been used with golden hamsters by Schiffman (1971). In this study, the animals were placed on the glass surface of the deep or shallow side, and the direction in which they moved was observed. No differences were noted in the direction of the subjects' locomotion after their initial placement on either side of the visual cliff. Therefore, the author concluded that tactual stimulation (i.e., continuous contact with the glass support) is more important than optical stimulation in controlling the animals' response to depth. A previous study (Schiffman, *et al.*, 1967) showed that rats used tactual information for depth discrimination when they had been placed on a real cliff apparatus. Similar results were obtained by Lore, *et al.* (1967) with rats tested on a physical cliff in conditions of total darkness.

In the present experiments, golden hamsters were submitted to four situations of depth discrimination, with conflicting cues corresponding to different sensory modalities (visual, tactual, and other possible cues). The aim of this procedure was to examine the subjects' preference for certain cues and to observe how they altered their choice of the deep or shallow side of the apparatus when presented with different combinations of perceptual cues.

Method

Subjects.—Twenty-five male and female golden hamsters, aged 2 to 5 mo., served as subjects.

Apparatus.—The basic apparatus has been described in detail by Etienne, *et al.* (1982). This apparatus is similar to a visual cliff apparatus, but without the transparent glass surface, and consists of a starting platform (40 × 20 cm) with a polyvinyl chloride (PVC) base and 30-cm high Plexiglas walls plus two wooden landing platforms (60 × 45 cm), each covered with PVC and a plastic sheet. Each landing platform was painted black and covered with a regular pattern of white dots (13 mm diameter), each dot spaced 3.4 cm from the other dots. A vertically-descending surface (16 cm high) was connected to the border of one side of the starting platform, providing the animals an apparently continuous support while they jumped from the starting platform on the corresponding side; see Fig. 2. This side was called "continuous;" the opposite side (without the vertical surface) was called "discontinuous." An infra-red video camera was used to observe the subjects in both infra-red and white light conditions. White light was provided by three 40-W bulbs placed 80 cm above the centerboard. Infra-red light was provided by a projector containing one 100-W halogen tube and one Shotfilter. The latter transmitted 50% light at 850 nm and 10^{-3}% light at 780 nm. Previous behavioral and electrophysiological experiments have shown that the hamster's visual responsiveness to red and near infra-red wavelengths ceases at 740 nm (Vauclair, *et al.*, 1977).

Procedure.—All subjects were tested in four phases, presented in the following order: Phase I, continuous/discontinuous choice in darkness with the two landing platforms located 50 cm from the starting platform; Phase II, continuous/discontinuous choice under light with the two landing platforms located 50 cm below the centerboard; Phase III, conflicting continuous/discontinuous choice in darkness with the continuous extremity of the starting platform leading to the deep side (landing platform at 105 cm) and the shallow side located 20 cm below the discontinuous extremity; and Phase IV, conflicting continuous/discontinuous choice under light. The conflicting aspect of Phases III and IV is based on a change (reversal) in the relation between height of the landing platform and the continuous extremity of the starting platform.

Familiarization with the apparatus was achieved only once, approximately 5 hr. prior to the beginning of Phase I; subjects were placed individually on the starting platform, with both landing platforms located 5 cm from the centerboard. All subjects were tested on the same day under a given condition (phase). An interval of four or five days separated the different phases. The subjects were tested in a random order for each phase. To avoid confounding side-effects, the apparatus was rotated 180° after two subjects had jumped. Both the starting and landing platforms were cleaned with alcohol after the completion of each trial.

All subjects were tested once in each phase. Each subject was placed on the center of the starting platform, with its head facing one wall. The animals were observed with the aid of a video monitor located in an adjacent room. The choice of the side and of the time spent on each extremity of the starting platform was recorded.

Results

Results concerning choices in the different phases are shown in Fig. 2. In Phase I, the animals relied predominantly on tactile support to descend from the starting platform in darkness. The tendency to use tactile cues was less pronounced, but still significant, when optical information was also available (Phase II). In Phase III, the majority of the subjects continued to use tactile support, even if this preference led them to the deep landing side. Finally, in the same situation, the animals reversed their preference under the influence of the optical choice criteria (Phase IV). In all four phases, the animals spent significantly more time on the side from which they ultimately left the starting platform (binomial test, $p \leq .001$).

The extent to which the animals shifted their choices from one phase of the

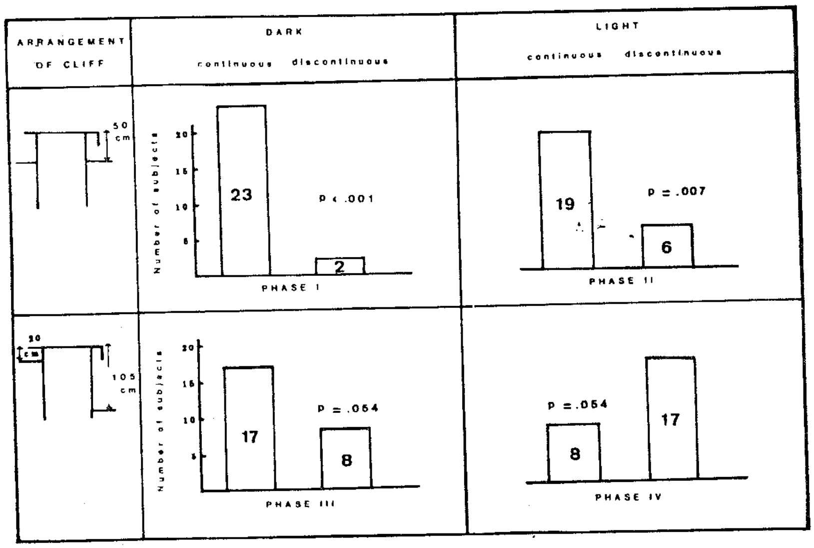

FIG. 2. Two arrangements of platforms (side view) and frequencies of choice ($n = 25$) for either the continuous or the discontinuous side in each phase. Statistics for each phase were computed with the binomial test.

experiment to another phase indicates the sensory modalities that are implied in depth perception. A comparison of a subject's choices in Phase I and in Phase II, when both landing platforms were at equal depth, shows that the presence of light did not alter significantly the animal's preference for the side of descent (binomial test, $p = .109$). The same comparison between Phases I and III, on the other hand, shows that in darkness, the animals changed their choice criteria and were no longer guided by tactile support if this support led to the deep landing side ($p = .016$). Finally, a comparison between Phases III and IV shows a significant shift ($p = .002$) from a predominance of tactile cues to a predominance of visual cues, the former leading to the distant landing side and the latter permitting the animals to choose the near side. An alternative explanation of the shift in preference in Phase IV from continuous to discontinuous is that the hamsters had discovered that the continuous side in Phase III results in a greater fall. However, the 4- to 5-day interval between Phases III and IV suggests that this is an unlikely possibility.

Discussion

Three important results have been obtained from the present experiments. First, tactile cues play a predominant role in the choice of the side from which subjects left the jumping apparatus. The predominance of tactile support under conditions of almost total darkness is decreased when visual information is also available. This result is in agreement with previous studies (Schiffman, 1971) which demonstrate the predominance of tactile over visual information on a normal visual cliff apparatus. Second, the complete shift of preference between Phases II and IV indicates that hamsters rely on visual information for depth perception if this information is available and represents a more adequate criterion for depth perception than tactile cues. This result also shows that the jumping apparatus used in these experiments represents a suitable device with which to test the hamster's visual perception of depth. Third, the changes in preference noted in Phase I compared to Phase III suggest that other types of cues interfere with tactile stimuli in a non-visual setting. Given the results of Exp. II and our previous findings on depth discrimination in darkness, it is suggested that, in the present experiments, acoustical information is used in conjunction with tactile and visual cues; for a detailed discussion of acoustical cues, see Etienne, *et al.* (1982).

It is possible to argue that olfactory cues might be used by hamsters to perceive differences in depth in the absence of optical and tactile cues; however, three viewpoints can be offered in opposition to this interpretation. First, Swann (1933), using the Lashley jumping platform to test the ability of rats to discriminate odors, showed no positive evidence that the subjects had learned to discriminate platforms on the basis of olfactory cues. According to Durup (1970), the hamster can be trained to orient towards an olfactory stimulus (the animal's own odor) located within 20 cm of the subject using a procedure involving the progressive removal of the stimulus from an initial distance of 6 cm. It is unlikely that this olfactory orientation could be performed in the present experiments, in which the landing platform contained non-specific olfactory information and the animals performed only one trial at a time. Second, in Exp. I, the hamsters were able to detect differences in height while in complete darkness and at distances ranging from 20 to 105 cm. Finally, hamsters with plugged ears did not choose the shallow landing side of a real cliff when tactile and optical cues were no longer present (Etienne, *et al.*, 1982). In summary, under test conditions used in the present research, golden hamsters are able to detect differences in height with the aid of only three sensory modalities, i.e., tactile, visual, and acoustical.

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Accepted January 5, 1984.