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Calibration of retinal image size with distance in the Mongolian gerbil: Rapid adjustment of calibrations in different contexts

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Mongolian gerbils were trained to jump from one platform to another across a gap whose size varied randomly from trial to trial. In test sessions, probe landing platforms differing in width from those used in training were used, and the distance that the animals jumped was measured. The first experiment demonstrated that the gerbils learned to calibrate the retinal image size of the landing platform with its distance and that they could learn more than one calibration at a time. The second experiment provided evidence that such calibrations are rapidly adjusted to environmental contingencies. These findings suggest that retinal image size might be a useful distance cue for gerbils in a variety of ecological contexts.

A growing body of evidence suggests that Mongolian gerbils are capable of estimating the absolute distance of visual objects with remarkable accuracy (Ellard, Goodale, MacLaren-Scorfield, & Lawrence, 1986; Ellard, Goodale, & Timney, 1984; Goodale, Ellard, & Booth, 1990). In this work an experimental task was used in which gerbils were required to jump from one platform to another. The distance between the two platforms ranged from about one to three body lengths and was varied randomly from trial to trial (see Ellard et al., 1984, for details). Not only do normal gerbils rarely fail to complete a jump in such a task, but they also display good economy of effort, seldom overjumping the edge of the landing platform by more than 2 or 3 cm. Most past work has been devoted to discovering the sources of visual information that allow gerbils to perform so well, and to study the ways in which gerbils might take advantage of multiple sources of distance information in a relatively unconstrained task.

Past work has shown that retinal image size (RIS) is an important source of distance information for gerbils (Goodale et al., 1990). In these experiments, gerbils were trained to jump to a landing platform of a particular and unvarying width. After training, the gerbils were presented with sets of *probe* trials embedded within a series of normal training trials. On the probe trials, landing platforms of different widths were substituted for the normal landing platform. The gerbils made errors that could be predicted on the basis of the assumption that they were using RIS information to calibrate the distance to the landing platform. That is, wider probe trials resulted in underjumps and narrower probe trials resulted in overjumps.

In order for retinal image size to be useful, it is necessary to have access to information about the real physical size of the goal object. In some cases, the sizes of goal objects may be relatively invariant. Such goal objects could include conspecifics, predators, or prey (Collett & Land, 1975; Via, 1977). In such cases, the calibration between image size and physical distance might be relatively stable over the lifetime of the animal. In other cases, the physical size of a goal object might be learned as the need arose through a series of exposures. Such cases would include the negotiation of environmental objects in a familiar home territory (Cartwright & Collett, 1979). Although both types of cases are worthy of investigation, the experiments carried out so far fall into the latter category.

If retinal image size is to be a generally useful source of distance information, it seems reasonable to expect gerbils to be able to learn more than one calibration at a time, and to use each calibration in the appropriate context. The purpose of the present set of experiments was to determine whether gerbils could learn such multiple calibrations and use them effectively.

EXPERIMENT 1

In this experiment, we set out to train gerbils to jump in two different contexts, using a different-sized landing platform in each one. In the test sessions, a probe landing platform was used that was approximately halfway in width between the landing platform used on one apparatus and that used on the other. In this experiment, therefore, the gerbils were required to learn two calibrations between retinal image size and physical distance and to use each of these calibrations in the appropriate context. In this case, the context consisted of a particular

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width of landing platform, as well as ambient visual information present in the room. Since the same landing platform was used for some of the probe trials in both contexts, we predicted that the gerbils would produce both overjumps and underjumps on these trials, depending only on the context in which the probe platform was presented.

Method

Subjects. Seven adult Mongolian gerbils (*Meriones unguiculatus*) were used. The gerbils were housed individually in Plexiglas cages and were provided with ad-lib access to water. Measured amounts of Purina lab chow were fed to the gerbils once every 24 h to keep them at approximately 90% of free-feeding weight. The gerbils were maintained on a 12:12-h light:dark schedule and were always tested during the light phase.

Apparatus. The jumping stand consisted of a takeoff platform (19 cm wide × 19 cm high × 30 cm long) and a set of five landing platforms ranging in width from 13.5 to 28 cm but with constant height (19 cm) and length (23 cm). The takeoff and landing platforms were placed on one of two tables in the testing room. Each table was illuminated from above, and a background was placed behind the landing platform at a constant distance of 80 cm from the leading edge of the takeoff platform. The background for one table consisted of randomly distributed filled black circles of varying size, and the background for the other table consisted of randomly distributed lines varying in length and orientation. The backgrounds were used to provide additional contextual information.

Training. The animals were divided into two groups ($n = 3$ and $n = 4$). One group was trained with the narrowest platform in one context and the widest platform in the other context. For the other group, the converse arrangement was used. Training consisted of placing the animal on the takeoff stand and placing a single sunflower seed on the landing platform, 3 cm from the leading edge. Initially, the takeoff stand and the landing platform were placed in contact with one another. Over the course of training, the mean distance between the takeoff and landing platforms was gradually increased, until all the gerbils could successfully and consistently jump a distance of 34 cm. During training, the context (and hence the size of the landing platform) was varied randomly from trial to trial.

Testing. Testing was conducted over 7 days. Each test session consisted of a set of 30 trials. Fifteen of the trials were conducted on each of the two jumping stands. Distances were varied randomly and ranged from 10 to 34 cm in 3-cm increments. On 18 of the trials, the same landing platform was used on each jumping stand as had been used for training. The remaining 12 trials were probe trials in which the usual landing platform was replaced by another platform of a different width. Three probe landing platforms were used (P1, width = 15.5 cm; P2, width = 20 cm; P3, width = 26 cm). Each animal received two probe trials at each of the distances 16, 22, and 28 cm on each of the two jumping stands. Each set of two such probe trials consisted of one trial with P2 and the other with either P1 or P3. P1 was used if the narrow training platform had been used on the jumping stand on which the trial took place. P3 was used if the wide training platform had been used on the jumping stand on which the trial was to take place.

On Test Days 1 and 4, the context in which a test trial took place was varied from trial to trial (*mixed* condition). On Test Days 2 and 3, the animals received 15 consecutive trials in one context and then 15 consecutive trials in the other context (*separate* condition). The order in which the two contexts were presented was counterbalanced among animals. Retraining sessions of 18 trials each were intercalated between testing days. On all such retraining days, the distance and the context were varied randomly from trial to trial. The purpose of these retraining days was to minimize the cumulative effect of repeated exposure to probe platforms during testing.

Analysis. The gerbils were videotaped using a CCD videocamera equipped with a high-speed shutter. Images from single frames of videotape were transferred to a microcomputer, using a frame-grabbing interface. The images were scaled and the touchdown location of the forepaws was measured. In the cases in which animals jumped short of the landing platform, touchdown location was taken to be the point at which the forepaws crossed the horizontal plane joining the takeoff and landing platforms.

Results

Figure 1 shows the effect of presentation of probes in each of the testing conditions (mixed and separate). As can be seen from the figure, the effect of presenting a smaller probe platform was to produce an overjump relative to control performance and the effect of presenting a larger probe was to produce a relative underjump [mixed, $F(3,18) = 8.68, p < .001$; separate, $F(3,18) = 55.2, p < .001$]. Furthermore, the size of the probe effect was related to the difference in size between the training platform and the probe platform. Smaller differences between these two platforms resulted in smaller deviations from control performance on probe trials. A comparison between testing conditions suggests that the probe effects in the separate condition were considerably larger than those in the mixed condition [$F(3,226) = 4.87, p < .01$], especially at longer distances.

Discussion

The results of Experiment 1 suggest that gerbils use retinal image size to calibrate the amplitude of jumps to visual objects. In the present experiment, as in previous work (Goodale et al., 1990), manipulations of the physical size of the landing platform produced systematic errors in jump accuracy that were related to the retinal image size of the object. Not only did the directions of these errors accord with our predictions (overjumps for smaller landing platforms and underjumps for larger landing platforms), but the magnitude of the differences was related to the size of the difference between probe and control landing platforms. As in previous studies, the absolute magnitude of the errors produced on probe trials was somewhat smaller than would be predicted if the gerbils were using retinal image size cues alone. This suggests that they are using more than one of the available sources of depth information in the task, and that they are weighting estimates that have been obtained from these multiple sources of information (Ellard et al., 1984; Goodale et al., 1990).

The data contain strong evidence that gerbils are able to learn more than one calibration between retinal image size and physical distance at a time, and to use each calibration in the appropriate context. The best evidence for this comes from the comparison of performance on probe trials for which large overjumps and large underjumps were predicted. It should be borne in mind that, for both of these sets of probe trials, the identical probe platform was used. This platform, being intermediate in size between the two training platforms, would be interpreted as being either closer to the animal or farther away from it, depending only on the control platform that the

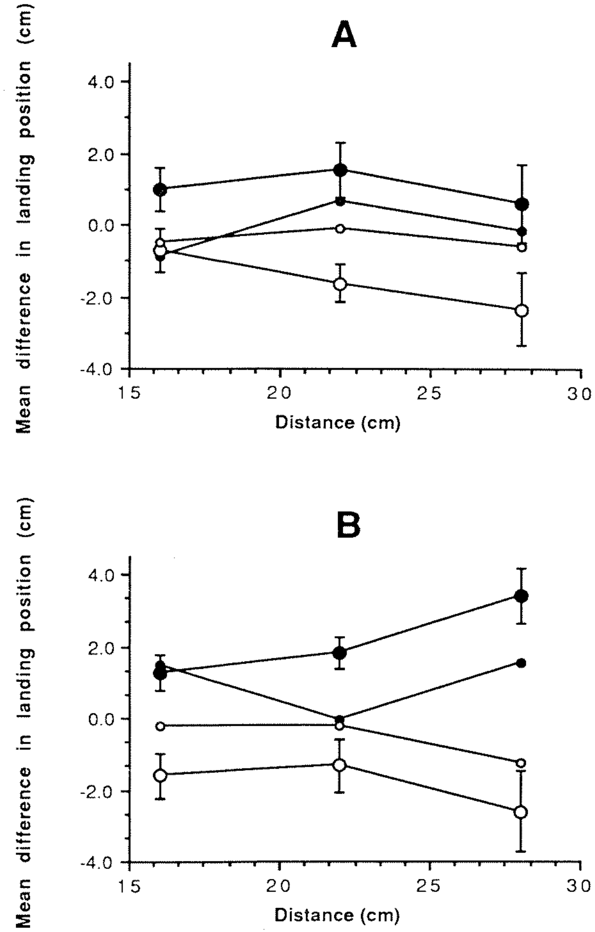

Figure 1. The effect of four different types of probe platform on landing position. Data are summed over animals. Each data point represents an average of difference scores. The difference scores were calculated by subtracting the landing position on a probe trial from the landing position on a control trial conducted on the same day, in the same condition, and at the same distance. Filled circles: trials where probe platforms were smaller than control platforms. Open circles: trials where probe platforms were larger than control platforms. Small circles: trials where probe platforms differed slightly from control platforms. Large circles: trials where the differences between control and probe platforms were larger. Error bars represent standard error and, for clarity, are shown only for trials with predicted large over- or underjumps. (A) Mixed condition. (B) Separate condition.

animal expected. The only guide to the formulation of this expectation would be the context in which the task was to be performed.

In general, the effect of probe trials was greater when the test sessions consisted of two sets of consecutive trials in each context than when the two contexts were presented randomly from trial to trial. A straightforward interpretation of this difference is that in the separate condition, the distance estimate obtained from retinal image size was weighted more heavily than it was in the mixed condition, perhaps because the reliability of an RIS estimate would correlate with the animals' ability to identify the context. Normally, a gerbil that was required to remember the sizes of objects on the basis of their locations would move from one place to another under its own control. This movement, and the sensory stimuli to which it would expose the animal, would likely be a rich source of information regarding its location. Although our procedures eliminated much of this information, there were more opportunities for the gerbils to recognize their location in the separate condition than in the mixed condition. When an animal is tested repeatedly in one context, its confidence that it *is* in that context and not another one will be likely to increase over the course of the testing session. Our mixed condition deprived the gerbils of the luxury of consistent exposure to a single context, and probably made it more difficult for them to determine where they were.

EXPERIMENT 2

In Experiment 1, we demonstrated that gerbils relied more heavily on retinal image size cues in the separate condition than in the mixed condition. One possible reason for this, as described above, is that repeated exposure to a single context increased the animals' confidence in a particular calibration. Another possibility is that, rather than retrieving calibrations on the basis of context, the gerbils were rapidly reformulating these calibrations using feedback from the immediately preceding jumps. In order to test this directly, we conducted a second experiment in which animals were trained using only one size of training platform. In the test phase, they were presented with a probe landing platform that was either larger or smaller than the training platform, for a block of nine trials. If gerbils are capable of rapidly forming RIS calibrations (as opposed to rapidly retrieving them), then we would expect to see evidence of this recalibration during the course of the nine successive probe trials in a session.

Method

Subjects. Five male 3-month-old gerbils were used. Housing and maintenance schedules were the same as those used in the previous experiments.

Procedure. The animals were trained to jump across a gap, using the operant methods described above. Initially, all animals were trained to jump to a platform 20 cm wide until they could successfully and consistently clear a 34-cm gap. Following this training regimen, the animals were required to complete a session of 19 jumps for 6 consecutive days. Each test session consisted of 5 trials with the training platform, followed by 9 consecutive trials with a probe platform and then 5 trials with the training platform. The distances used for each trial were randomized, but for each session, the distances used for the last training trial (A1), the first probe trial (B1), the last probe trial (B2), and the first training trial after probes (A2) were identical. Each animal was tested in one session in which each of the distances 16, 22, and 28 cm occurred in these trial positions. Hence, each animal received a total of three test sessions. The order of distance presentations at critical trial locations was randomized among animals. Three retraining sessions were inserted between the test sessions in order to minimize day-to-day carryover effects. These retraining sessions consisted of 19 trials with randomized gap distances but with the same landing platform for each trial.

The animals received the test regimen described above twice. For one series of sessions, a probe platform smaller than the training platform was used (13.5 cm wide), and for the other series of sessions, a larger probe platform was used (28 cm wide). Three animals were tested with the larger probe platform first, and 2 animals were tested with the smaller probe platform first.

Results

Figure 2 shows the mean landing positions of animals on Trials A1, B1, B2, A2, summed over all distances tested.

Strong probe effects were seen both when a smaller landing platform was substituted [$F(3,15) = 8.23$, $p < .002$] and when a larger platform was used [$F(3,15) = 6.50$, $p < .005$]. The smaller probe platform caused a significant overjump on Trial B1 relative to Trial A1 performance (Newman-Keuls, $p < .05$). There were no other significant differences between trial positions, although the difference between B1 and B2 (both on the probe platform) fell just short of significance ($p < .1$). When the larger probe platform was used, significant underjumps occurred on B1 relative to A1 ($p < .05$), and these underjumps had been corrected by B2 ($p < .05$). Substitution of the training platform on A2 caused significant overjumps relative to both B2 (probe platform) and A1 (training platform) ($p < .05$ for both comparisons). The effect of trial day was not significant for either larger or smaller probe platforms [$F(2,32) = 2.06$ and 1.97, respectively]. There was no evidence for an interaction between trial day and probe type [$F(6,32) = 0.49$ and 0.33 for smaller and larger probes, respectively].

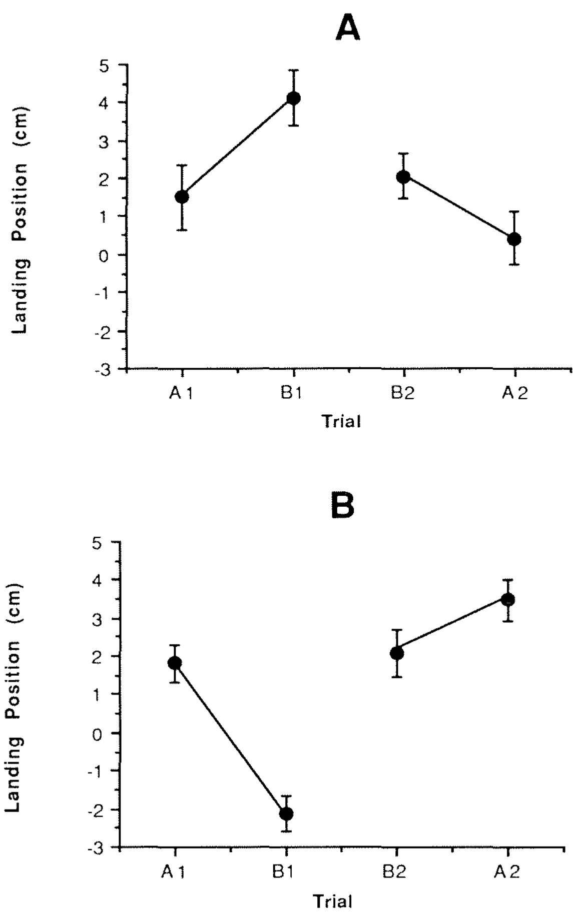

Figure 2. Mean landing position for four different trials in Experiment 2. A1 is the last trial with the standard landing platform before switching to the probe platform. B1 is the first trial on the probe platform. B2 is the last trial on the probe platform. A2 is the first trial after switching back to the standard platform. Data are summed over 3 test days, three distances, and all animals. Error bars represent standard errors of mean. (A) Standard platform is replaced with a smaller probe platform. (B) Standard platform is replaced with a larger probe.

Discussion

It is not at all surprising that strong retinal image size effects were observed in the transition from A1 to B1 in this experiment. These effects were present in both conditions (larger or smaller probe trials) and were very similar to effects that have been observed under similar conditions both in the present set of experiments and in earlier work. Much more interesting is the difference between mean landing position on B1 and B2. All intervening test trials were conducted on the same-sized landing platform, and the gerbils proved to be able to compensate for the change in platform size over the course of nine trials, such that their landing position on B2 was about the same as it had been before any probe manipulations. This rather rapid recalibration is reminiscent of that seen in previous work (Goodale et al., 1990). Even more compelling evidence that recalibration has taken place is seen in the differences between landing positions on B2 and A2. The appearance of an image size effect running in the opposite direction to that seen at the A1/B1 transition suggests that the recalibration that the gerbils carried out involves more than merely changing the force of the jump on the basis of feedback from previous trials, and must also take into account the visual angle subtended by the landing platform.

In summary, the results of Experiment 2 provide evidence that rapid calibration is possible. By presenting gerbils with an entirely new landing platform for only nine trials, we were able to produce probe effects that were indistinguishable from those usually seen after many weeks of training animals to use one particular calibration.

GENERAL DISCUSSION

The experiments reported here provide further evidence that retinal image size is a useful cue to absolute distance in the Mongolian gerbil. The results suggest that gerbils are capable of using RIS information in two ways that have not been investigated directly until now. In Experiment 1, we showed that gerbils could learn two separate calibrations between the visual angles of objects and the force required to jump to those objects. We also showed that gerbils were able to retrieve the correct calibration in the appropriate context. The best evidence for this was the presence of significant probe effects in the mixed condition in Experiment 1, in which gerbils were randomly moved from one context to another on a trial-by-trial basis. Finally, in Experiment 2, we showed that gerbils were able to recalibrate RIS information very rapidly.

Together, these findings suggest that retinal image size may be a more useful source of distance information for gerbils than might otherwise have been assumed. The first finding suggests that gerbils in their natural habitat can use retinal image size to judge the distance to a number of objects. This type of skill might be particularly useful for an animal that requires frequent and accurate updates of its location with respect to salient environmental features, such as the location of refuges. The second finding suggests that even in cases in which a gerbil has had no previous exposure to a particular object, it is capable of forming a calibration between RIS and distance very rapidly. Since a great deal of gerbil behavior (and animal behavior in general) involves repetitive movements from one place to another (foraging and hoarding, for example), there would probably be ample opportunity to form such calibrations as the need for them arose.

In light of the multiplicity of sources of depth information in any three-dimensional visual array, it is somewhat surprising that so little attention has been paid to mechanisms that might serve to combine these sources in an optimal way. Perhaps the most ambitious attempt in this regard was the work of Freeman (1966, 1970). To our knowledge, Freeman was the first to make the distinction between the two types of factors that might contribute to the relative weighting of visual information in a depth task. Most of his work was devoted to the investigation of the optical and geometrical limitations of depth cues (psychophysical factors), but he also suggested that other types of factors such as perceptual learning and expectancy (psychogenic factors) might operate in a depth task as well. More recently, Collett and Harkness (1982) have given a brief quantitative treatment of one possible mechanism of cue combination based on information theory, but they were primarily concerned with optical and geometric factors. Although cue conflict studies are presently rather popular (Braunstein, Andersen, Rouse, & Tittle, 1986; Nawrot & Blake, 1989), they are most often used in human psychophysical studies to test for dependencies among depth cues (in studies of aftereffects, for instance) rather than to study the ways in which behaving animals might normally integrate several independent pieces of information. In our work, gerbils are forced to make a single computation of absolute distance on each trial. In this way, we can obtain quantitative estimates of perceived distance that are scaled relatively directly. Furthermore, by presenting misleading distance information for one particular cue, and by manipulating the reliability of that information, it has been possible to examine the operation of both types of factors involved in combining distance estimates.

REFERENCES

Braunstein, M. L., Andersen, G. J., Rouse, M. W., & Tittle, J. S. (1986). Recovering viewer-centered depth from disparity, occlusion, and velocity gradients. *Perception & Psychophysics*, **40**, 216-224.

Cartwright, B. A., & Collett, T. S. (1979). How honey-bees know their distance from a nearby landmark. *Journal of Experimental Biology*, **82**, 367-372.

Collett, T. S., & Harkness, L. I. K. (1982). Depth vision in animals. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfield (Eds.), *Analysis of visual behavior* (pp. 67-110). Cambridge, MA: MIT Press.

Collett, T. S., & Land, M. F. (1975). Visual control of flight behaviour in the hoverfly (*Syritta pipiens L.*). *Journal of Comparative Physiology*, **99**, 1-66.

Ellard, C. G., Goodale, M. A., MacLaren-Scorfield, D., & Lawrence, C. (1986). Visual cortical lesions abolish the use of motion parallax in the Mongolian gerbil. *Experimental Brain Research*, **64**, 599-602.

Ellard, C. G., Goodale, M. A., & Timney, B. (1984). Distance estimation in the Mongolian gerbil: The role of dynamic depth cues. *Behavioural Brain Research*, **14**, 29-39.

Freeman, R. B., Jr. (1966). Function of cues in the perceptual learning of visual slant: An experimental and theoretical analysis. *Psychological Monographs*, **80**(Whole No. 610), 1-29.

Freeman, R. B., Jr. (1970). Theory of cues and the psychophysics of visual space perception. *Psychonomic Monograph Supplements*, 3(13, Whole No. 45), 171-181.

Goodale, M. A., Ellard, C. G., & Booth, L. (1990). The role of image size and retinal motion in the computation of absolute distance by the Mongolian gerbil (*Meriones unguiculatus*). *Vision Research*, **30**, 399-413.

Nawrot, M., & Blake, R. (1989). Neural integration of information specifying structure from stereopsis and motion. *Science*, **244**, 716-718.

Via, S. E. (1977). Visually mediated snapping in the bulldog ant: A perceptual ambiguity between size and distance. *Journal of Comparative Physiology*, **121**, 33-51.

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