

## Visual modulation of vestibularly-triggered air-righting in the rat

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Unlike cats, which can initiate righting in the air either with vestibular or visual input alone, the rat is dependent solely upon the labyrinths to trigger this response. We show, however, that the rat can modulate the onset and speed of its rotation according to the height above the ground from which it is dropped. In the absence of vision, rats initiate rotation with a latency of about 50 ms, irrespective of the height from which they are dropped. With vision, rats can modulate their latency to begin rotation, from about 102 ms at 50 cm, to about 39 ms at 7.5 cm. Similarly, as height of release decreases, the speed of rotation (i.e. degrees/ms) increases. Thus, in rats, even though vision cannot trigger air-righting, it does adaptively modulate this behavior as an allied reflex, increasing the likelihood that the animals will land on their feet.

### INTRODUCTION

For species such as cat<sup>6</sup> and monkey<sup>5</sup>, vision or labyrinths alone are capable of initiating righting in the air. In contrast, only the labyrinths can trigger this response in lower mammals such as rats and guinea pigs<sup>3,5</sup>. However, in studies of the ontogeny of the air-righting reflex in the cat, Carmichael<sup>1</sup> revealed another role for vision in this response. Depending upon the starting height, visual input can modulate the speed of righting, so that the animals right faster when falling from a smaller distance<sup>9</sup>. Because vision is not sufficient to trigger righting in species such as rat and guinea pig, it has apparently been assumed that vision plays no role in their air-righting, since no investigation has been made of this possibility. In this paper, we show in the rat that even though vision cannot trigger air-righting, it does modulate

its latency and speed, depending upon the height from which the animal is dropped.

### MATERIALS AND METHODS

#### *Subjects*

Fourteen male Long-Evans Hooded rats weighing 350–450 g were used. The animals were obtained from Charles River Animal Laboratories (Wilmington, MA). They were housed individually at a constant room temperature of 21–23 °C, on a 12 : 12 h light/dark cycle, lights on at 07.00 h. Experiments always began between 16.00 and 17.00 h. Food and water were provided ad libitum.

#### *Visual occlusion*

In order to block vision, opaque acetate contact lenses were inserted under the eyelids. For inser-

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tion, a drop of xylocaine was administered to the cornea, and another was placed inside the contact lens<sup>2,7</sup>.

#### Experimental procedure

Each rat was tested, with eyes open, at 4 heights above the ground, 50 cm, 25 cm, 15 cm and 7.5 cm; 10 trials per height. Then each rat was retested in the same way with eyes occluded. The rats were dropped supine onto a foam cushion. Prior to being dropped, the animals were held upside down by the shoulders and by the pelvis, from beneath, and were not released until they ceased struggling and remained relaxed in the experimenter's fingers. The air-righting trials were recorded on videotape using a Panasonic (WV-D5000) strobe video camera, with the strobe effect shutter having a speed of 1/1000 second for exposure every 1/60 second. This provided high resolution blur-free frames for analysis of the movement at a speed of 30 frames/s.

#### Analysis

Successful air-righting was scored when the rat landed in a prone position, with at least 3 limbs contacting the ground with their ventral surface (i.e. palm or sole). Righting was divided into two parts, (1) latency to begin rotation (from the frame at which the rat was released to the frame at which the animal began to rotate), and (2) speed of rotation (from the frame when rotation first began until the frame when rotation no longer occurred). The animals were dropped so that the camera had a lateral view. From this position, movement of the rat's head towards or away from the observer could be used as a marker for onset of rotation. Similarly, cessation of rotation could be identified by the absence of any change from one frame to the next. Speed of rotation was calculated as degrees rotated per ms for those trials in which the rat completed a 180 degree turn, from supine to prone. Latency to begin rotation could be compared at all 4 heights, but since only two rats righted successfully at the lowest height when occluded, only the 3 highest heights were used for comparison. The video frames were counted and converted to the nearest millisecond (ms). For this study two of the subjects were used for

preliminary testing, so that the numerical data presented are based on the other 12 animals.

#### RESULTS and DISCUSSION

Since repeated righting trials from the same height could have modified the animals' righting behavior due to feedback from how they landed, only the first trial for each height was used to calculate the latency of onset of rotation. In this way only the visual contribution to the change in drop height was assessed. When vision was intact, the mean latency to begin rotation at 50 cm was 102 ms; at 7.5 cm it was 39 ms (Fig. 1; Friedman two-way analysis of variance:  $\chi_r^2 = 30.8$ ,  $df = 3$ ,  $P < 0.001$ ). When vision was occluded there was no decrease in latency of onset of rotation with decreased drop height. Instead, at all heights, they began to rotate at about the same latency (48~55 ms; Fig. 1;  $\chi_r^2 = 3.7$ ,  $df = 3$ ,  $P > 0.05$ ). Similarly, when vision was intact the speed of rotation during righting also increased significantly as drop height decreased, but not when vision was occluded (Table I). Since the first successful righting trial was not necessarily the first trial for each drop height, for Table I all successful righting trials were used to calculate

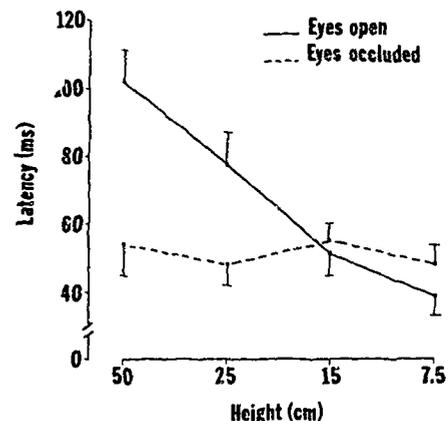


Fig. 1. Latency to begin righting when dropped supine in the air. The mean ( $\pm$  S.E.M.) latency at each height is based on the first trial for each rat. Therefore, any change with drop height is solely dependent upon vision, and not from information based on repeated drops from the same height. With eyes open, the rats show decreased latency with decreasing drop height, whereas when the eyes are occluded no change in latency with drop height was present.

TABLE I

Speed of rotation (degrees/ms) from supine to prone with decreasing drop height

Data are means  $\pm$  S.E.M.

	Drop height			Friedman 2-way analysis of variance
	50 cm	25 cm	15 cm	
Eyes open ( $n = 12$ )*	1.13 (0.04)	1.30 (0.03)	1.58 (0.08)	17.28, $P < 0.001$
Eyes occluded ( $n = 10$ )	1.23 (0.04)	1.28 (0.04)	1.40 (0.04)	1.40, $P > 0.05$

\* Number of rats which righted successfully at all heights and hence were used for across heights comparisons.

individual mean speed of rotation, which was than used to calculate group means. Therefore, this measure may also include feedback from repeated falls from the same height. However, given the large difference between non-occluded and occluded rats (Table I), most of this change in speed of rotation with decreasing drop height appears to be due to visual input.

After a long latency, and thus a long fall, when the animal begins to rotate, it is falling faster than immediately upon release. As suggested by one of the reviewers this might require a greater turning speed than when turning from rest. If the increased speed of rotation with decreasing drop height (Table I) is due to the physics of falling and not due directly to visual modulation of righting speed, then it would be predicted that at any drop height there should be a negative correlation between latency and speed of rotation. That is, rats with the longest latencies should have the fastest speeds. Such comparison (using Spearman rank correlations) for the 3 highest heights revealed no significant correlation between latency and speed in either rats with vision (50 cm:  $r_s = 0.12$ ,  $n = 12$ ,  $P > 0.05$ ; 25 cm:  $r_s = -0.19$ ,  $n = 12$ ,  $P > 0.05$ ; 15 cm:  $r_s = -0.27$ ,  $n = 12$ ,  $P > 0.05$ ) or those without vision (50 cm:  $r_s = -0.18$ ,  $n = 12$ ,  $P > 0.05$ ; 25 cm:  $r_s = -0.08$ ,  $n = 12$ ,  $P > 0.05$ ; 15 cm:  $r_s = -0.22$ ,  $n = 10$ ,  $P > 0.05$ ). We conclude that the change in speed with decreasing drop height results from direct visual modulation, not the physics of falling. Therefore, both with respect to latency to begin rotation (Fig. 1) and the speed of

rotation (Table I), vision modulates air-righting in the rat.

These visually mediated changes in air-righting appear to be adaptive, since with decreasing drop height, more rats with vision righted successfully

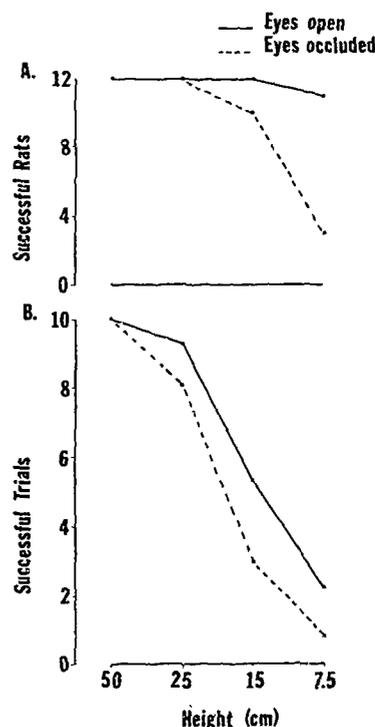


Fig. 2. Success in air-righting is compared between rats with eyes open and eyes occluded. A: of the 12 rats tested, the number successfully righting at least once was greater with eyes open than with eyes occluded. B: although the mean number of successful righting trials decreased with decreasing height for both sighted and visually occluded animals, the decrement in success rate was greater, at all heights, for the visually occluded animals.

(Fig. 2A) on more trials (Fig. 2B) than did rats with vision occluded.

It might be argued that at the highest heights the rats are more fearful and hence freeze, thus delaying righting, and that this is not an adaptive visual modulation as such. Taking the occluded animals as the baseline for initiation of righting in the absence of fear, it can be seen that they begin to right equally fast at all drop heights (Fig. 1). When dropped at the lowest heights (15 and 7.5 cm), as is also indicated in Fig. 1, rats with vision showed a shorter latency than those animals with vision occluded. This difference was significant at 7.5 cm (Wilcoxon matched-pairs signed ranks test: for  $Z = -1.69$ ,  $P < 0.05$ ). The sight of the close-looming ground appeared to promote righting rather than inhibiting it due to any possible fear-induced freezing. Therefore, at the very lowest height, rats could use vision to alter the latency to begin rotation (Fig. 1) and the speed of rotation (Table I) in a seemingly adaptive way, in order to land successfully (Fig. 2). Whether the rats are inhibited by fear in initiating and in speed of rotation at the highest height is still a question. To us it seems more reasonable to assume that at the highest heights, the rats see that they have plenty of time before they need to right, and that it is simply less pressing to right at the highest heights, but more urgent at the lowest ones.

Developmentally, in kittens, Warkentin and Carmichael<sup>9</sup> showed that at first vestibularly-triggered air-righting occurred in the absence of vision. After eye-opening, the modulating role of vision preceded the ability of the eyes to trigger air-righting independently of the labyrinths. This raises the possibility that, developmentally, in rats also, vision at first has no role, but later may begin to modulate air-righting. Indeed, when young rats first begin to right themselves in the air, they are initially more successful when dropped at greater heights<sup>4</sup> indicating that they are not increasing

their speed of righting at lower heights. We hypothesize that at this early stage of development (about 14 days, or so) sighted rats should right at constant speed irrespective of the height at which they are dropped, as is the case for occluded adult rats (Fig. 1). Only later in development (about 23–25 days), when distant visual cues are responded to<sup>8</sup>, would we expect that visual modulation of speed of righting will emerge.

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