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Short Communications

Air righting without the cervical righting reflex in adult rats

Sergio M. Pellis*, Vivien C. Pellis* and Philip Teitelbaum

Department of Psychology, University of Florida, Gainesville, FL 32611 (U.S.A.)

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The current explanation of air righting in animals is that when falling supine in the air, labyrinthine stimulation triggers head rotation. The head rotation involves neck rotation which, via the cervical righting reflex, triggers rotation of the body. (In cats and monkeys, when the labyrinths are absent, visual stimulation when falling supine can also trigger this righting sequence.) In the present paper, a descriptive analysis of air righting in the rat shows that the shoulders rotate, carrying the unmoving head and neck passively along. Thus, for this species, labyrinthine input appears to trigger shoulder rotation directly, independently of the cervical righting reflex. This suggests that at least two physiological mechanisms exist for labyrinthine control of head rotation during air righting, one via the neck and the other via the shoulder girdle.

In all animals studied so far, righting in the air appears to use a mechanism of which the details were worked out by Magnus[6].

> 'In summarizing this work Magnus suggests that the ability to turn in the air so as to land on all fours is a function of intact labyrinths. The typical course of falling in a normal cat, as determined from pictures which Magnus himself has taken and reproduced, involves a series of stages including the following: First, the animal falls for a short distance through the air, back down. The head then begins to turn while the rest of the body remains undisturbed. When the head has turned through 90 degrees the thorax begins to turn, the hind portion of the body still remaining immobile. Soon, however, this rear portion begins to turn, and finally the body is completely re-oriented, so that the animal lands on all four legs. This landing is made possible because the tonus and extension of the limbs have undergone change, as if in preparation for this landing, during the latter part of the fall. In an analysis of this complex act Magnus suggests that the reaction of the receptors of the labyrinth is essential in initiating the head turn and that this turning then initiates tonic neck reflexes which lead to complete body turning' (from Carmichael[1], p. 455).

In short, as Fukuda[4] sums it up, the labyrinthine reflex triggers the cervical righting reflex which promotes the turning of the torso and the rest of the body.

In cats[8] and monkeys[6], vision in the absence of the labyrinths can also trigger head righting, when falling supine in the air. In rats, only the labyrinths, not vision, can trigger righting in the air[2]. Cats[3,16] as well as rats[11], however, can modulate the latency of onset and speed of righting visually, so as to adjust this reflex adaptively to the height of the fall. Thus, the standard textbook model is that head righting recruits the body via the cervical righting reflex, whether triggered by the labyrinths or by vision[7,9,14].

While studying this phenomenon in the rat we found that righting in the air appears to be mediated directly by the shoulder girdle; the head and the neck do not turn actively but are merely carried unmoving by the shoulder girdle. This suggests that at least two physio-

* Present address: Department of Psychology, The University of Lethbridge, Lethbridge, Alberta, Canada T1K 3M4.
Correspondence: S.M. Pellis, Department of Psychology, The University of Lethbridge, Lethbridge, Alberta, Canada T1K 3M4.

logical mechanisms exist for labyrinthine control of head rotation during air righting, one via the neck and the other via the shoulder girdle.

Fifteen adult male Long Evans Hooded rats were used (300–450 g). They were individually housed at a constant temperature of 21–23 °C, on a 12:12 h light/dark cycle, lights on at 07.00 h. Experiments were conducted between 11.00 and 17.00 h, in the rats' light phase. Food and water were provided ad libitum.

Rats were held supine, by the shoulders and the pelvis, and dropped onto a soft cushion from a height of 40 cm. In each trial the rat was held until it relaxed, and when dropped its head was approximately perpendicular to the ground (see Fig. 1). Care was taken not to impart any angular momentum to the rat when released. For 12 rats, the righting trials were recorded on a Panasonic (WV-D5000) video camera, with a strobe effect shutter having a speed of 1/1000 second for exposure every 1/60 second. This provided blur-free frames for analysis of the movement at a speed of 30 frames/s. Each rat was dropped at least 6 times. For two rats, the righting trials were recorded on a 16 mm movie film, using a Lo Cam Camera at 500 frames/s. Each rat was dropped 2–4 times. (Movie film taken at 150 frames/s were also available for 8 rats from a previous study[10].) Finally, for one rat, 4 trials were recorded on video at 1/1000 second shutter speed at a speed of 1000 frames/s using a Kodak Ektapro 1000 computer-based, high speed video system. In about half of the righting trials the rats were filmed laterally, and in the remainder they were filmed head on.

Detailed, frame-by-frame analysis of 6 trials from the 500 frames/s movie film and of the four trials that were videorecorded at 1000 frames/s revealed that the head and neck never rotated before the shoulders. In each trial, the shoulders rotated to prone, carrying the head and neck along passively. This is illustrated in tracings made from photographs taken from high speed video (1000 frames/s) in Fig. 1. Inspection of an additional 70 trials from the other videotaped and filmed material supported this observation. Therefore, in the adult rat, as far as we can tell, the head and neck do not rotate actively when righting in the air.

Of course, this is not to say that head turning via neck rotation during righting does not exist in the rat. Firstly, on the ground, it can be seen when righting is triggered by tactile stimulation of the snout[12,13]. With the snout continuously in contact with the ground during rotation, the head and neck turn first, followed sequentially by the shoulders and the rest of the body. However, when righting on the ground is triggered by asymmetrical tactile input on the body, in the absence of snout contact, the shoulders rotate, carrying the head and neck passively to prone[12].

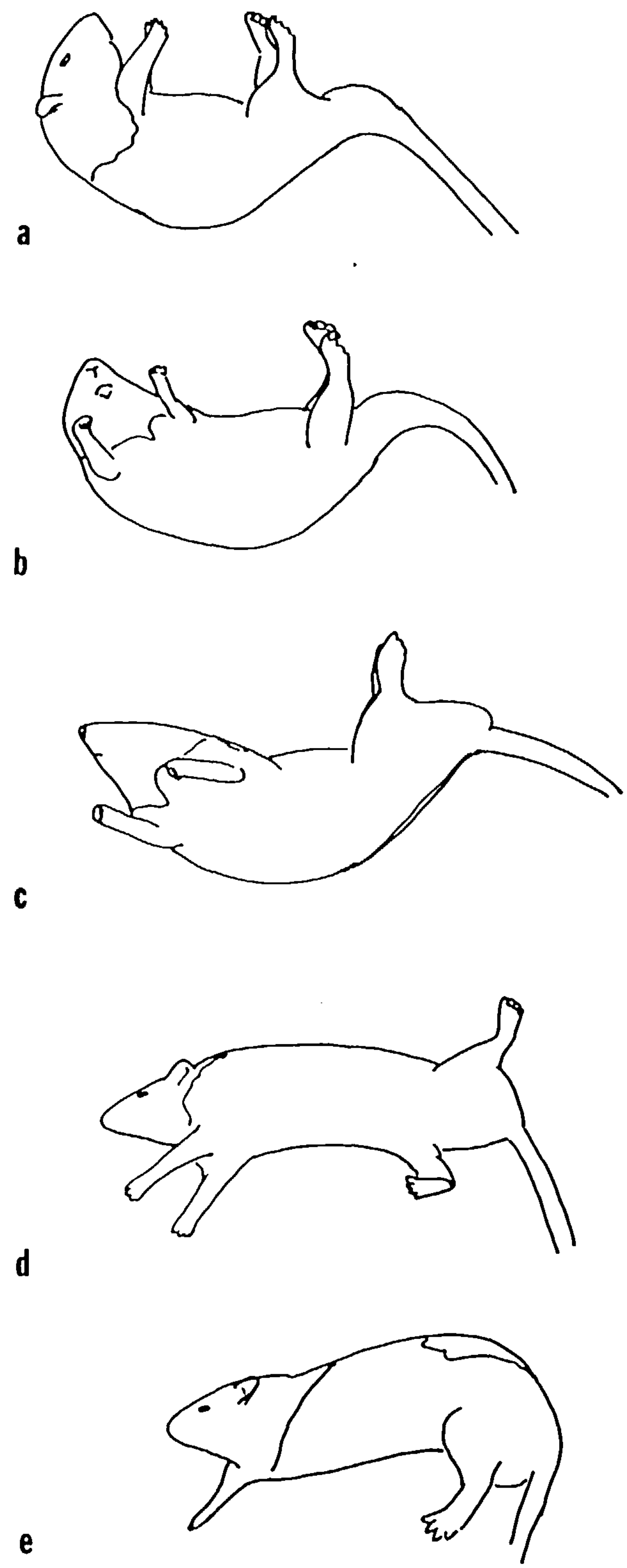

Fig. 1. Tracings from photographs taken from the video monitor show a righting sequence in which the rat was dropped laterally with respect to the camera. In the first photograph (a), the rat is shown immediately upon release so that its head and feet point skyward. Upon release, the forepaws are tucked up to the sides of the face, and then the head, neck and shoulders rotate en bloc toward prone (b and c). Once the forequarters are nearly prone, the hindquarters are still 90° from prone (d), but then active pelvic rotation brings the remainder of the body to prone (e).

Secondly, during the ontogenesis of air righting in rats[5], as in rabbits and cats[15,16], the head and neck are the first to rotate, and then several days later, the shoulders rotate following the head and neck. From this it may be thought that early in development, in all species, the shoulders are recruited via the cervical righting reflex. In adulthood, cats and rabbits continue to recruit the shoulders via the cervical righting reflex (see above), whereas for adult rats, head rotation is inhibited. Our preliminary observations on golden hamsters and the marsupial, *Dasyurus hallucatus*, show that in these species, the head, neck and shoulders also rotate en bloc during air righting. Indeed, some observations suggest that adult rabbits also rotate the head, neck and shoulders en bloc[17]. Thus, the rat does not appear to be the only species in which vestibular air righting is achieved via shoulder rotation, without active head rotation.

The difference between species that do, and those that do not rotate their necks during air righting may be accounted for by two possibilities. One is that there are two mechanisms in air righting; neck rotation is dominant in some species (e.g. cat, rabbit) and shoulder-led righting is dominant in others (e.g. rat, hamster). An alternative possibility is suggested by a recent developmental study of the rat by Laouris et al.[5]. They state that even in infancy, the cervical righting reflex may not be responsible for triggering shoulder rotation. They analysed the development of air righting in rats tested with a harness that prevented independent head, neck and shoulder rotation, and compared them with rats which were unrestrained in this manner. If the shoulder rotation during air righting in infant rats were actually caused by the preceding head and neck rotation, one would expect that in a harness that prevented independent head and neck rotation, independent shoulder rotation should be clearly delayed. However, in the unrestrained pups, head and neck rotation occurred as early as about 5 days; and shoulder rotation, following head and neck rotation, occurred by about day 7. In the harnessed infants, shoulder rotation also commenced at day 7, suggesting that the developmental onset of shoulder rotation may not depend upon the cervical righting reflex. Therefore, for the rat, there is no independent evidence for shoulder rotation being recruited via the cervical righting reflex when falling supine in the air. Throughout all this early developmental period, however, such cervical recruitment appears to be present during righting on the ground when the snout contacts the ground (see above). In order to verify that in such instances (on the ground) neck rotation is necessary for the recruitment of shoulder rotation, a harness that blocks independent head, neck and shoulder rotation, as used by Laouris et al.[5], would be necessary. The same reasoning applies to the supposed recruitment of the shoulders by neck rotation found in cats and rabbits. The observation that head and neck rotation precedes shoulder rotation is not, then, sufficient evidence to conclude that neck rotation triggers shoulder rotation. Physically preventing the neck from rotating when falling supine, by application of neck cast or brace, would be necessary in order to determine whether shoulder-led rotation can occur in species where it is ordinarily not seen, such as the cat.

Our results on adult rats support those of Laouris et al.[5] in showing that neck rotation is unnecessary for triggering shoulder rotation during air righting. This is counter to the idea that the physiological mechanism proposed by Magnus is the only one that operates in righting. Nonetheless, Magnus (1924) did provide experimental evidence for such a mechanism. That is, if the head and neck of a cat held by the pelvis is rotated by the experimenter, then the shoulders are recruited, and also rotate. This is true for a bilabyrinthectomized and blind-folded cat, showing that the shoulder recruitment is via the cervical righting reflex. Clearly, neck rotation is sufficient to recruit shoulder rotation. What is at issue here is whether in the cat such a cervical righting reflex is necessary to right when falling in the air. For the rat, it appears not to be.

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