

## Labyrinthine and visual involvement in the dorsal immobility response of adult rats

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The dorsal immobility response (DIR) is typically seen in the infants of many altricial mammalian species. Lifting the animal into the air by the nape of the neck is the primary releasing stimulus. Functionally, this response appears to facilitate carrying of the infants by the adults. When grasped by the nape and lifted into the air, adult rats will also exhibit the DIR. In this paper, the role of the labyrinths in the DIR of adult male rats was examined. Vestibular stimulation produced by vertical circular acceleration increased the duration of the DIR, while labyrinthectomy greatly diminished the DIR. In rats with intact labyrinths, visual occlusion greatly potentiated the DIR, whereas, in labyrinthectomized rats, visual occlusion had little effect. These data indicate that the vestibular system plays a major role in mediating the DIR of adult rats. The retention of the DIR into adulthood and the possible increased role of the labyrinths in the control of the adult DIR, are discussed with respect to the possible role of the DIR as an anti-predator mechanism.

### INTRODUCTION

Retrieval of displaced infants by picking them up orally is a widespread phenomenon among mammals, especially for species with altricial young where the adults are basically quadrupedal and have restricted dexterity of the forelimbs<sup>25</sup>. The antiquity of this response is indicated by its occurrence in the most conservative of eutherian mammals (e.g. tenrecs, elephant shrews)<sup>8</sup>. In many species, such retrieval involves a specialized response by the infant as well. For example, when an infant or juvenile rat is retrieved by its mother or by another adult, it typically remains immobile in a ventroflexed posture, with its limbs tucked into its body<sup>1,5</sup>. The effective stimulus for this dorsal immobility response (DIR) is tactile pressure on the skin of the nape<sup>1</sup> which can be

achieved not only by an adult rat's teeth, but also by an experimenter's fingers or by a clamp<sup>6,13</sup>. Brewster et al.<sup>1</sup> demonstrated that in the absence of the DIR, the mother found it more difficult to transport the young. Although mothers and other adult rats typically do not carry pups older than 40 days<sup>6</sup>, rats continue to exhibit the DIR well into adulthood<sup>17</sup>. Not only rats, but the adults of many species of non-domesticated muroid rodents also retain the DIR as adults<sup>30</sup>. This suggests that the retention of the DIR by adult rats is not an aberrant manifestation of domestication; a process which typically produces adults with more juvenile-like characteristics<sup>4</sup>. Rather, it suggests that the retention of the DIR in adulthood may serve some different function. One possibility that has been proposed for other forms of immobility responses (e.g. tonic immobility;

death feigning), is that the DIR in adulthood may serve an anti-predator function<sup>11,12</sup>.

Irrespective of its functional significance, the DIR induced by holding adult rats by the skin of the nape and lifting them into the air has proven to be a useful measure for pharmacological analysis<sup>17,27,28</sup>. However, it appears that the DIR of adults may be neurochemically different to that of infants. For example, haloperidol, a dopamine antagonist, greatly enhances the duration of DIR in adult rats<sup>17</sup>, whereas it diminishes the duration of DIR in infant rats<sup>33</sup>.

Differences between the DIR of infants and adults may provide important clues about the function this response assumes in adulthood. For example, De La Cruz and Junquera<sup>5</sup> recently showed that circular acceleration potentiates the duration of immobility and intensifies limb flexion in adult rats but not infants and juveniles. This demonstration indicated that vestibular input can modulate the DIR. Indeed, De La Cruz and Junquera<sup>5</sup> suggested that the labyrinths play a more significant role in the onset and duration of the DIR in adults than in infant and juvenile rats. However, swinging a rat through the air stimulates more than just the vestibular apparatus, so that the finding by De La Cruz and Junquera<sup>5</sup> could have been produced by the proprioceptive/tactile stimulation involved in such a procedure. In the experiments reported here, we tested part of this hypothesis by comparing the DIR of intact adult rats with that of labyrinthectomized adult rats. If the labyrinths play a significant role in the DIR of adult rats, then the DIR of labyrinthectomized adult rats should be diminished.

## MATERIALS AND METHODS

### *Subjects*

Forty male Long-Evans hooded rats, obtained from Charles River Laboratories (Wilmington, MA) were used. They weighed between 500 and 600 g. They were housed individually with continuous access to food and water available in a 21–23 °C room maintained on a 12:12 h light/dark cycle (lights on at 07.00 h). All testing began at 14.00 h.

### *Chemical labyrinthectomy*

Labyrinthectomies were performed by the method of Horn, DeWitt and Nielson<sup>12</sup>. The rats were first anesthetized (0.33 ml/100 mg b.wt. Equithesin anesthesia; a chloral hydrate and sodium pentobarbital mixture), and then 20 mg/kg (concentration = 100 mg/ml) of sodium arsanilate (Abbott, Chicago, IL) was injected through the tympanic membrane into each middle ear (intratympanically). Following each injection, the external auditory passage was packed with Gelfoam (UpJohn, Kalamazoo, MI). The effectiveness of each labyrinthectomy was confirmed behaviorally on the following day by loss of air-righting, reduced postural support, the presence of exaggerated head dorsiflexions, and the inability to orient to gravity when placed supine in a tank of water<sup>3,19</sup>. In a previous study, it was shown that in addition to these behavioral markers (which are the same deficits exhibited by surgically labyrinthectomized rats), histological evidence indicated that eighth nerve degeneration follows this chemical procedure<sup>3</sup>. The controls received the same treatment, but did not receive the sodium arsanilate injections. After recovery from the anesthesia, the controls did not show any of the vestibular deficits.

### EXP. 1

In order to test the effects of the labyrinths on the DIR, two forms of stimulation were provided. In the first, the rats were picked up by the nape and swung back and forth, thus providing dual stimulation of the skin of the nape and presumably of the labyrinths. This test provided both of the stimuli previously shown to increase the duration of the DIR<sup>1,5</sup>. In the second, the rats were picked up by the shoulders (i.e. the skin was not pinched and the nape was untouched) and also swung back and forth. If vestibular stimulation in adult rats is an important factor in the DIR response, then it would be expected that vestibular stimulation alone should cause some degree of immobility. Furthermore, if the vestibular apparatus is critical to the DIR, then the DIR should be abolished by labyrinthectomy.

**Subjects:** Ten intact and 10 labyrinthectomized rats were used.

**Procedures:** Prior to each of the following tests, the rats were placed supine in a 90° V-shaped trough for 30 s. They were then grasped and lifted so that no part of their bodies touched any other surface. Each rat was tested sequentially in the following ways: (1) It was grasped by the nape of the neck (between the ears and the shoulders) and lifted into the air. In this procedure, a DIR was always elicited immediately; (2) It was picked up in the same manner and swung back and forth at arm's length for about 90° on each swing, at about one swing/s for 10 s. (3) It was picked up by the shoulders, so that the experimenter's fingers grasped behind the forelegs and around to the chest, and was lifted into the air; (4) It was picked up by the shoulders (as in (3)), and then swung back and forth as in (2).

Because the DIR was immediately elicited, the duration of the response was measured from its onset until the animal displayed escape-like behavior; or until 300 s had elapsed. Each animal received 3 trials for each test with an intertrial interval of 30 s. Individual means based on these 3 trials were used to calculate group means. In addition, a qualitative assessment was made of the body posture each animal adopted when exhibiting the DIR: this involved noting the position of the limbs, whether they were tucked into the body or extended out from the body. Still photographs (35 mm) were taken with an AE-1 Canon programmable camera.

### Results

For intact rats, there was a significant difference between the method of being picked up ( $F = 48.74$ , d.f. = 1,18,  $P < 0.001$ ), the presence of vestibular stimulation ( $F = 42.80$ , d.f. = 1,18,  $P < 0.001$ ), and their interaction ( $F = 12.40$ , d.f. = 1,18,  $P < 0.01$ ) (Fig. 1). For labyrinthectomized rats there was a significant difference between the method of being picked up ( $F = 79.79$ , d.f. = 1,18,  $P < 0.001$ ), but no significant effect in swinging them (Fig. 1). Subsequent analysis (Newman-Keuls tests) of the interaction showed that picking the rats up by the nape of the neck was more effective than picking them up by

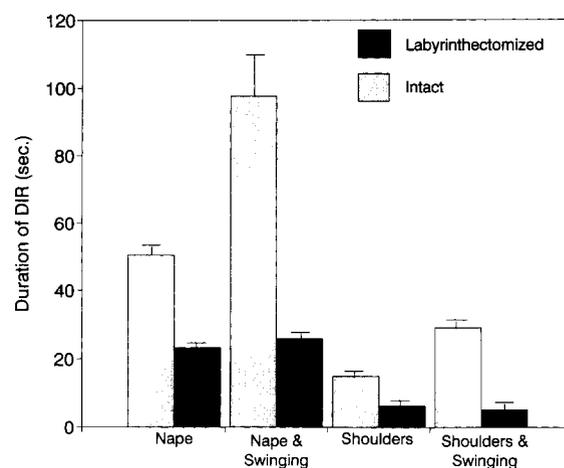


Fig. 1. Histograms show the mean ( $\pm$  S.E.M.) duration of immobility in intact and labyrinthectomized rats when picked up by the nape or the shoulders, with and without being swung back and forth.

the shoulders ( $q = 4.77$ ,  $P < 0.05$ , for intact rats;  $q = 14.17$ ,  $P < 0.001$ , for labyrinthectomized rats). Furthermore, for intact rats, there was a significant increase in the duration of the DIR after being swung when held by the nape ( $q = 6.35$ ,  $P < 0.001$ ), but not when held by the shoulders ( $P > 0.05$ ). Picking up the labyrinthectomized rats by the nape produced a significantly longer duration of immobility than picking up intact rats by the shoulders ( $t = 13.54$ , d.f. = 9,  $P < 0.001$ ). However, intact rats that were held by the shoulders and then swung, increased the duration of their immobility to levels similar to those of labyrinthectomized rats that had been picked up by the nape.

During the DIR, there was also a marked difference in the posture of the intact vs the labyrinthectomized rats. The intact rats kept their limbs flexed up against their bodies (Fig. 2A). In contrast, the labyrinthectomized animals extended their limbs outward (Fig. 2C). This difference in posture was apparent in every intact and labyrinthectomized rat tested. Furthermore, although each intact rat flexed its limbs during the DIR, the tightness of this flexing varied between animals. However, if they were swung back and forth, the limb flexion tightened and in many cases the lower body ventroflexed (Fig. 2B). Simply



Fig. 2. Posture adopted during the DIR. A: intact animals tuck their limbs into their body. B: this limb tucking is further enhanced by gentle vestibular stimulation. C: labyrinthectomized animals extend their limbs outward away from their body.

picking the intact rats up by the nape produced postures ranging from that seen in Fig. 2A to that seen in Fig. 2B; the addition of swinging them, made all the intact subjects adopt the posture seen in Fig. 2B. Swinging the labyrinthectomized rats did not alter the outward extension of their limbs.

#### Discussion

The peripheral vestibular apparatus appears to exert a major effect on the DIR. Its stimulation, by swinging, greatly potentiated the duration and form of the DIR, and its destruction greatly diminished the duration of the DIR, and abolished the posture typical of this response. These data support the hypothesis by De La Cruz and Junquera<sup>5</sup> that vestibular stimulation plays a dominant role in the expression of the DIR in adult rats. However, the comparison between lifting the rats by the nape and by the shoulders illustrates that the potentiating effects of vestibular stimulation is small unless the nape is pinched. That is, vestibular stimulation by itself has little effect in producing the DIR, but rather has a highly significant effect in potentiating the DIR once it is triggered by pinching the skin of the

nape. Nonetheless, with a larger sample size the increased immobility induced by swinging the rats by the shoulders would probably be significant, since we routinely use this technique to calm rats down prior to hypodermic injections.

#### EXP. 2

It is possible, of course, that the labyrinthectomy may have disrupted the expression of the DIR due to an indirect effect. For example, labyrinthectomized rats tend to be hyperactive (Porter, Pellis and Meyer, in preparation), and exhibit more head movements<sup>3</sup>. Such hyperactivity might have indirectly interfered with the DIR. Since visual occlusion has a calming effect on animals (e.g. covering the eyes of captured wild rats with a black cloth calms them<sup>23</sup>), we reasoned that visual occlusion might similarly affect our rats and hence enhance the DIRs, even in labyrinthectomized animals. Accordingly, we measured the DIRs of both intact and labyrinthectomized rats with and without visual occlusion.

*Subjects:* Twenty intact and 20 labyrinthectomized rats were used.

**Procedure:** Prior to the DIR test on day 1, 20 new rats, not used in Exp. 1, were tested. Five normal and 5 labyrinthectomized rats were fitted with visual occluders; the other 5 normal and 5 labyrinthectomized rats were not. On day 2, each rat was tested in the other visual treatment condition.

**Visual occlusion.** Opaque, acetate contact occluders were inserted under the rats' eyelids in order to block their vision<sup>2</sup>. A drop of lidocaine was administered to each cornea and another drop was placed inside each contact occluder prior to its insertion<sup>2,19</sup>.

An additional control group was used to determine the effects of the occluders. The 20 rats from Exp. 1 were used following the same procedures described above for Exp. 2. However, in this case, lidocaine was administered to the rats' corneas without inserting the occluders.

### Results

Because there was no significant difference between days 1 and 2, the data were pooled for a  $2 \times 2$  factorial design analysis for the 20 rats receiving the occluders. The main effects for the duration of DIR are shown in Fig. 3. There was a significant difference between the control and labyrinthectomized rats ( $F = 129.96$ , d.f. = 1,36,  $P < 0.001$ ) as well as a significant occlusion effect ( $F = 67.72$ , d.f. = 1,36,  $P < 0.001$ ) and significant interaction between labyrinthectomy and occlu-

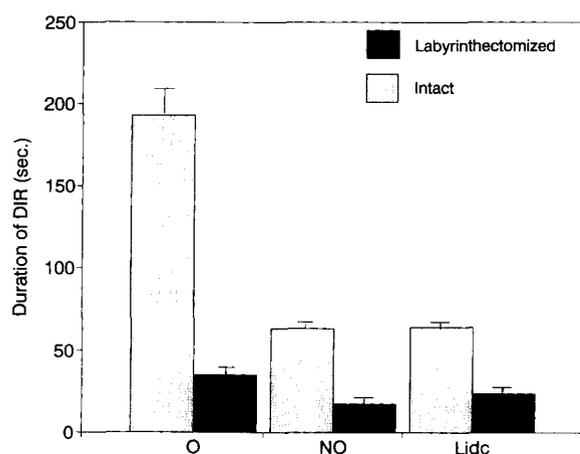


Fig. 3. Histograms show the mean ( $\pm$  S.E.M.) duration of DIRs in intact and labyrinthectomized rats, with (O) and without (NO) visual occlusion, and with lidocaine (Lidc).

sion ( $F = 38.96$ , d.f. = 1,36,  $P < 0.001$ ). Subsequent analysis (N-K tests) of the interaction showed that there was no significant visual occlusion effect for the labyrinthectomized rats ( $P > 0.05$ ), whereas visual occlusion significantly potentiated the DIR in normal control rats ( $P < 0.05$ ). Labyrinthectomy attenuated the DIRs in both occluded and non-occluded rats. Administration of lidocaine, without the occluders, had no effect in either intact or labyrinthectomized rats (Fig. 3).

### Discussion

Visual occlusion profoundly potentiated the DIR of intact rats. However, such potentiation was weak and non-significant for labyrinthectomized rats. Anesthetizing the eyes in the absence of the occluders had little or no effect, demonstrating that visual blockade was responsible. These findings indicate a previously unsuspected role for vision in the DIR and in addition, further support those of Exp. 1 in implicating the vestibular apparatus as a major factor in the control of the DIR in adult rats.

### GENERAL DISCUSSION

Exp. 1 replicated the findings of De La Cruz and Junquera<sup>5</sup>, showing that by swinging adult rats, after lifting them into the air by the nape, the DIR is significantly increased. Indeed, swinging the rats, in the absence of gripping the skin of the nape, had a significant effect on the duration of the DIR. The hypothesis that such swinging potentiated the DIR by stimulating the labyrinths<sup>5</sup> was supported by the demonstration that labyrinthectomy greatly diminished the duration of the DIR (see Fig. 1). In addition to reducing the duration of the DIR, labyrinthectomy also abolished the typically flexed posture of the DIR present in intact rats (see Fig. 2). Even though gripping labyrinthectomized rats by the nape of the neck and lifting them into the air produced a shorter-duration DIR compared to that of intact rats, it produced a significantly longer-duration DIR compared to the labyrinthectomized rats that had been held in the air by the shoulders (Fig. 1). Taken together, these findings suggest

that vestibular stimulation produced in adult rats by swinging them back and forth, potentiates the DIR produced by pinching of the nape.

Brewster and Leon<sup>1</sup> demonstrated that anesthetizing the skin of the nape of the neck blocks the DIR in infant rats. Tactile stimulation of skin areas of other parts of the body were much less effective<sup>1</sup>. However, such stimulation potentiates the DIR when in conjunction with pinching the nape<sup>6</sup>. Indeed, even an airpuff onto the venterum can potentiate the DIR produced by pinching the nape<sup>32</sup>. In the present experiment, simply lifting the rats by the nape of the neck, without added vestibular stimulation, produced a significantly longer DIR in intact rats than in labyrinthectomized rats. This suggests that the duration and form of the DIR is to a large part dependent upon the integrity of the peripheral vestibular apparatus.

Before this hypothesis is accepted, however, other possibilities need to be considered. The most obvious is that labyrinthectomized rats are hyperactive, performing frenetic movements, especially with the head<sup>3</sup>. This may interfere indirectly with the DIR. For example, we have found that in the first few days following labyrinthectomy, adult rats will walk backwards, swinging their heads laterally and backward in seemingly uncontrolled ballistic movements. Visual occlusion stops these uncontrolled head movements, and the rats walk forward, and apart from some ataxia, they appear normal (S. Pellis, V. Pellis and P. Teitelbaum, work in progress). Therefore, in Exp. 2, in an attempt to reduce hyperactivity following labyrinthectomy, the rats were tested for the DIR when visually occluded. Although the mean duration of the DIR was doubled for labyrinthectomized rats, it was not significantly different to when they were tested with vision (see Fig. 3). In contrast, visual occlusion had a significantly greater effect in intact rats. Indeed, blocking vision produced a 3-fold increase in the duration of the DIR (see Fig. 3). Considering the minor role of vision in guiding rat behavior<sup>20,26,31</sup>, the magnitude of this effect is surprising. Indeed, Wilson<sup>32</sup> showed that a light flash stimulus failed to potentiate or diminish the DIR produced by nape pinch in young rats. The

experiment with visual occlusion, while not conclusive, supports the view that the labyrinths play a major role in the expression of the DIR. Nonetheless, we cannot think of any experiment in which the confounding role of hyperactivity can be eliminated, and hence test the direct effect of the labyrinths on the DIR. Overall, however, the results presented here all strongly implicate an important and perhaps direct role by the labyrinths in the DIR of adult rats.

The labyrinths not only appear to potentiate the DIR when stimulated, as suggested by De La Cruz and Junquera<sup>5</sup>, but also seem necessary for the full expression of this response in adult rats (see Figs. 1–3). Given that vestibular stimulation produced less of an effect on the DIR in 10–20-day-old pups<sup>5</sup>, we predict that the DIR of infant rats should be less affected by labyrinthectomy. It would be of interest to compare labyrinthectomized and intact infants to identify the age at which vestibular input becomes the major component in the DIR. Nonetheless, whether this difference between the DIR in juveniles and adults can ultimately be attributed to the labyrinths or not, it is clear from the results by De La Cruz and Junquera<sup>5</sup> and from the present paper, that being swung through the air potentiates the DIR of adult rats.

Two further questions arise from this study and that of De La Cruz and Junquera<sup>5</sup>. Why do adult rats retain the infantile DIR, and why is there a shift to a seemingly dominant control over this response by the labyrinths? Both questions may be related to predation. Most small-to-medium-sized mammalian carnivores (e.g. polecats, cats, foxes) kill rat-sized prey by biting the nape of the neck<sup>9,10</sup> and in many cases lift the prey up and apply predatory head shakes<sup>15,18</sup>. Therefore, the pattern of predatory attack would provide the appropriate tactile and vestibular stimuli to induce DIR. Importantly, immobility by the prey appears to inhibit the release of the killing response in the predator<sup>7,24</sup>. For example, in a recent study of predatory behavior by cats<sup>21</sup>, we observed an instance where a cat pounced upon a mouse and delivered a nape bite. The mouse remained immobile while being lifted up and held in the cat's mouth. The mouse continued to lay

immobile on the ground after being released. After a few seconds, the mouse stood up and ran across the enclosure; its movement immediately triggering a renewed attack by the cat. This time, it resulted in a fatal bite to the mouse's nape. In many instances continued struggling of the mouse while being held in the cat's mouth was important in triggering a killing bite by the cat<sup>21</sup>. Such examples illustrate the value of immobility as an anti-predator strategy<sup>11,22</sup>.

The hypothesis that the DIR is retained in adulthood as an anti-predator strategy is further supported by its widespread occurrence in the adults of many species of muroid rodents<sup>30</sup>. The occurrence of a DIR-like behavior in the lizard *Anolis carolinensis*, produced by pinching the skin of the nape and lifting them into the air<sup>29</sup>, also supports the idea that the DIR is an anti-predator behavior, since such reptiles do not retrieve and carry their infants as do many mammals. Indeed, the demonstration of a DIR-like behavior in a lizard suggests that the DIR did not evolve in the context of parental retrieval<sup>29,30</sup>, but rather, that the DIR first evolved for its anti-predator function, and only later with the advent of altricial mammalian young, did the DIR become co-opted for its use as a facilitator for parental carrying. However, the absence of both oral retrieval by adults<sup>8</sup> and DIR in the young of marsupials (S. Pellis and V. Pellis, unpublished observations on the small carnivorous marsupial *Dasyurus hallucatus*) complicates the matter, since both eutherian and marsupial mammals share a common reptilian ancestry. Nor is this hypothesis supported by the early disappearance of this response in juvenile guinea pig-like rodents<sup>14</sup>, even though such animals presumably are subject to predation. However, guinea pigs do exhibit the tonic immobility response<sup>16</sup>, indicating that perhaps the kind of immobility response used by adults reflects the type of predators they have been subjected to during their evolution. Clearly, the evolutionary history of the DIR remains obscure. Nonetheless, the shift in rats from a purely tactile control in infancy, to a strong potentiation and even control by vestibular input in adulthood, may reflect the shift between the pup retrieval and the anti-predator functions of the DIR.

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