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Pharmacological Subtraction of the Sensory Controls Over Grasping in Rats

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PELLIS, S. M., V. C. PELLIS, D. P. O'BRIEN, F. DE LA CRUZ AND P. TEITELBAUM. *Pharmacological subtraction of the sensory controls over grasping in rats.* PHYSIOL BEHAV 39(1) 127–133, 1987.—Catecholamine-depletion-induced catalepsy isolates and leaves intact an aggregate of allied reflexes (e.g., righting, standing still, bracing, and clinging) which involve all the body and limb segments in defending stable static equilibrium [15]. Because other movement subsystems (locomotion, orienting, scanning, directed use of mouth or forepaws) are depressed, such animals cling in a vertical position for an abnormally long period of time. As a consequence, grasping reflexes may be studied independently of other responses. Haloperidol, a dopamine antagonist, abolishes visually elicited reaching and grasping, but leaves intact tactile and proprioceptive control of grasping. The grasping of haloperidol-treated rats can be further simplified by the pharmacological removal of the remaining sensory controls. The addition of morphine to haloperidol abolishes tactile grasping, while the addition of diazepam to haloperidol abolishes both tactile and proprioceptive (traction-elicited) grasping. Although visual, tactile, and proprioceptive grasping are abolished by haloperidol-plus-diazepam, some vestibular input to clinging remains: such rats, in response to being held vertically upright in the air, flex their digits with sufficient strength to allow them to cling vertically. The strength of forepaw digit flexion is severely diminished by labyrinthectomy, but the digits of the hindpaws appear to be unaffected. This residual non-labyrinthine digit gripping appears to be induced by proprioceptive inputs from the head, neck and torso in response to the vertical body position. Wrapping an elastic bandage snugly around the head and neck of a labyrinthectomized rat given haloperidol-plus-diazepam further diminishes the strength of forepaw digit flexion, and to a lesser degree hindpaw digit flexion. Application of an elastic bandage around the abdomen diminishes the strength of hindpaw digit flexion and to a lesser extent that of the forepaws. The application of both bandages simultaneously completely abolishes the digit flexion of both fore and hindpaws. Therefore, there appears to be a residual digit flexion in the haloperidol-plus-diazepam-treated rat which is controlled by labyrinthine and proprioceptive (head, neck and torso) mechanisms.

Haloperidol-induced catalepsy Grasping Labyrinthectomy Diazepam Morphine
Sensory controls over grasping

A characteristic feature of catecholamine-depletion (or blockade)-induced catalepsy is that animals (cats, monkeys, rats) will maintain a vertical clinging position for abnormally long periods of time [6, 17, 22, 23], due to a disinhibition of tonic grasping [3, 13]. Therefore, the catecholamine-depleted animal is a simplified preparation in which grasping can be elicited and maintained without the interference of other responses, such as climbing [5,15]. For example, when held upside down in the air, gerbils [21] or rats [14] treated with haloperidol (a dopamine antagonist) will grasp and hold a thin wooden rod which is gently placed in their paws. Such grasping can be elicited by gentle tactile stimulation of the ventral surface of the paw, and, once triggered, is maintained for two or more minutes. The tactile elicitation of grasping is also reinforced by proprioceptive stimuli from the forelimbs, and possibly by proprioceptive neck and vestibular stimuli when clinging vertically [2]. Therefore, in catalepsy, while grasping is maintained in isolation from other responses, such as climbing, and although it is simplified, in that visual control is not present [1,23], the remaining sensory controls are still complex.

The sensory control of grasping, already isolated in

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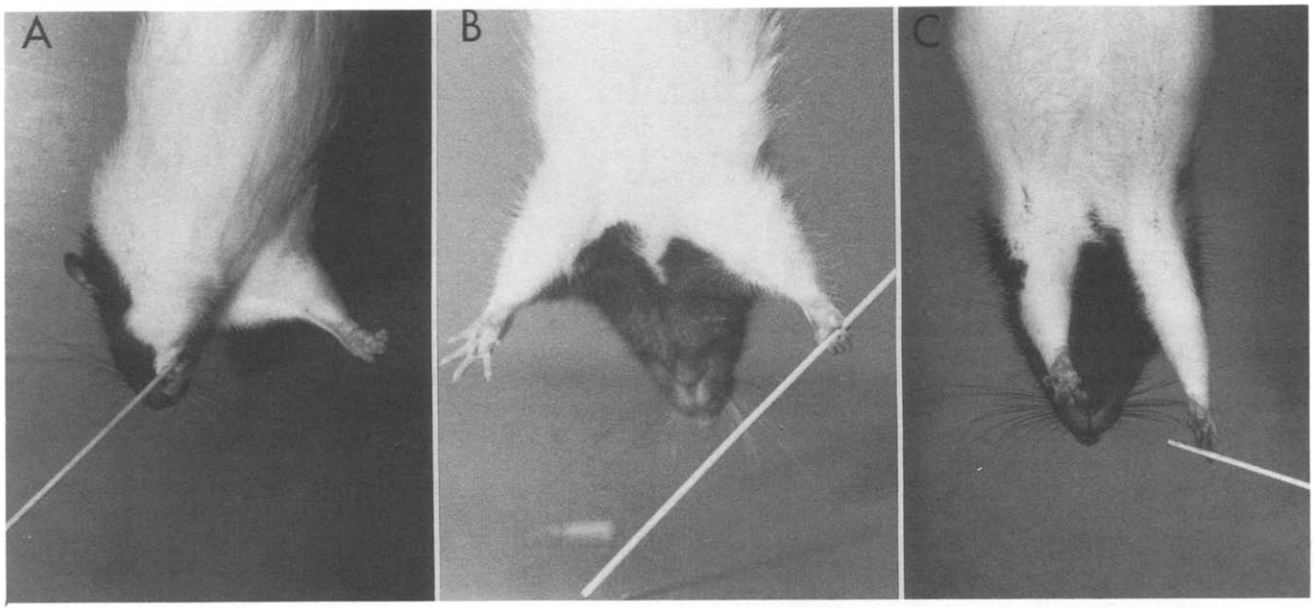

FIG. 1. Upside down grasping is shown by (A) a haloperidol-treated rat, in which the wooden rod is gripped firmly with the forepaw and the arm flexed against the body. In haloperidol-plus-morphine-treated rats (B) the grasp is only elicited by traction of the phalanges, and is restricted to flexion by the digits. In haloperidol-plus-diazepam-treated rats (C) no grasping response is elicited.

haloperidol-treated rats, can be further simplified by the addition of morphine or diazepam. Adding morphine to haloperidol abolishes tactile grasping, leaving intact proprioceptive grasping in response to traction of the digits [12]. The addition of diazepam to haloperidol abolishes both tactile and proprioceptive grasping [10]. In the latter the digits are flexed when the rat is held vertically upright, which in this paper is further investigated by the use of labyrinthectomy and bandaging of the head, neck and torso. Also, the sequence of loss and reinstatement of the sensory controls over grasping are described for haloperidol-treated rats given either morphine or diazepam. The sequence of reinstatement is shown to be similar to that described for humans in normal infantile development and in adult recovery after cerebral damage [18,19].

METHOD

Animals Used

Thirty-six male Long Evans hooded rats, weighing between 300–400 g were used. They were housed individually at a constant room temperature of 21–22°C, under a 12:12 hr light-dark cycle. Food and water were available ad lib.

Labyrinthectomy

Sodium arsanilate (Abbott, North Chicago) was injected intratympanically at a dosage of 20 mg/kg using a concentration of 100 mg/ml of sodium arsanilate dissolved in 0.9% saline, following the method of Horn, DeWitt and Neilson [7]. After each ear was injected, the external auditory passage was packed with Gelfoam (UpJohn Co., Kalamazoo). Our own studies show that this dose is highly effective in producing permanent vestibular damage [2]. Labyrinthectomies were performed while the rats were under 0.33 ml/100 g Equithesin (a mixture of chloral hydrate and sodium pentobarbital) anaesthesia. Testing began 4–5 days after surgery. The success of the labyrinthectomy was assessed by the loss of ability to air-right, reduced postural support, and the presence of exaggerated vertical head dorsiflexions during exploratory locomotion [1,8]. Histological and behavioral verification of successful chemical labyrinthectomy have been discussed in detail elsewhere [2].

Drugs Used

Morphine sulfate (Mallinckrodt) was dissolved in saline (0.9%), the dosage being calculated as the salt. Haloperidol (Haldol, McNeil) was available in 5 mg/cc ampules. Diazepam (Hoffmann-LaRoche) was dissolved in 40% propylene glycol and 10% ethyl alcohol, and mixed in concentrations of 5 mg/cc. All injections were administered intraperitoneally in volumes of 1 ml/kg.

Experimental Procedure

Thirty rats were given 5 mg/kg haloperidol, 6 of them received 20 mg/kg morphine in addition, and 22 of them received 5 mg/kg diazepam in addition to haloperidol. Thirteen of the rats given haloperidol-plus-diazepam were labyrinthectomized. Two rats were given an equal volume of saline alone. Thirty min after drug administration, their grasping behavior was tested (see below). Then the rats were tested again after having a bandage wrapped snugly around the head and neck alone, or around the abdomen alone, or around both areas simultaneously. An elastic bandage (ACE, Becton-Dickinson, New Jersey), 3 cm wide and 15 cm long, was used.

Behavioral Tests

Grasping by the forepaws was tested in two ways: (1) the

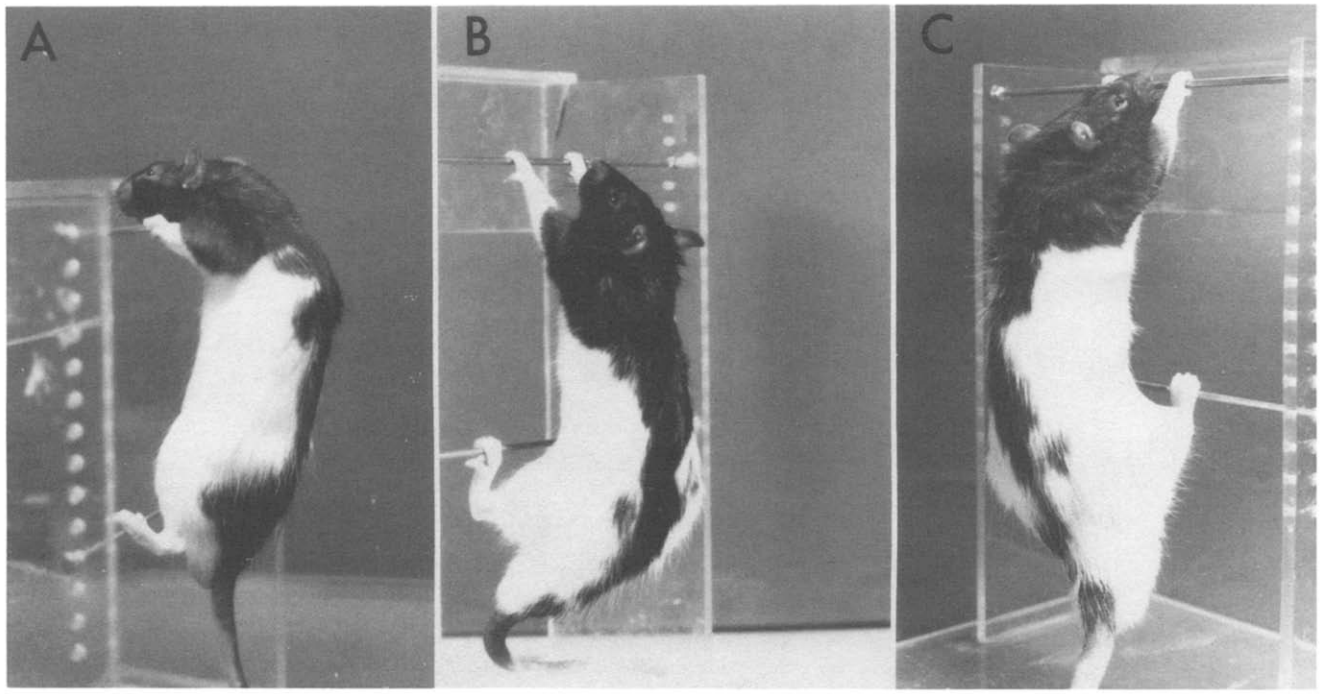

FIG. 2. Upright clinging in haloperidol-treated rats (A) shows the full forepaw grasp, complete with a "pull-up" flexion by the forelimbs, a "push-up" extension by the hindlimbs, and ventroflexion of the head. In haloperidol-plus-morphine-treated rats (B) and haloperidol-plus-diazepam-treated rats (C) clinging is restricted to the digits, with the body sagging downward.

rats were held upside down in the air by the tail, and a wooden rod, 2 mm in diameter and 20 cm long, was placed against the ventral surface of the digits and palm [21]. If touch failed to elicit grasping, the wooden rod was pressed against the digits, pulling them downward, so that the phalanges were stretched; (2) the rats' ability to cling vertically was tested by placing them on two horizontal stainless steel bars 2 mm in diameter and 8 cm vertically apart, mounted in a Plexiglas frame [17]. Thirty-five mm still photographs were taken to record the responses and postures in each test.

RESULTS

Grasping With the Forepaws

When the rats were held upside down by the base of the tail or by the pelvis, a wooden rod placed close to, but not touching, the forepaws elicited reaching and grasping in saline-treated rats, but not in haloperidol-treated rats. Administration of haloperidol alone was therefore sufficient to abolish visually elicited reaching and grasping.

While held upside down, all haloperidol-treated rats grasped a wooden rod that was gently placed onto the ventrum of the front paw or digits. Gentle tactile stimulation was sufficient to elicit this response, which involved the whole arm being flexed up against the body (Fig. 1A). When a haloperidol-plus-morphine-treated rat was held upside down, gentle tactile stimulation of the ventrum of the forepaw or digits was insufficient to elicit grasping; traction on the digits was required to elicit flexion of the phalanges. The grasping elicited by traction in the haloperidol-plus-morphine-treated rats was restricted to the digits with the forearm left extended (Fig. 1B). When a haloperidol-plus-diazepam-treated rat was held upside down, neither tactile nor proprioceptive stimulation of the hand or digits elicited grasping (Fig. 1C).

In summary then, haloperidol abolished visual grasping, haloperidol-plus-morphine abolished visual and tactile grasping, and haloperidol-plus-diazepam abolished visual, tactile, and proprioceptive grasping.

Clinging Vertically

When placed on the horizontal clinging bars, all the haloperidol-treated rats clung by grasping the upper bar with the forepaws and the lower bar with the hindpaws, coupled with a "pull-up" flexion by the forelimbs, a "push-up" extension by the hindlimbs, and ventroflexion by the head (Fig. 2A). All haloperidol-plus-morphine-treated rats clung only by the digits of the fore- and hindpaws with the body sagging downward (Fig. 2B). Unexpectedly, haloperidol-plus-diazepam-treated rats also clung with the digits of the fore- and hindpaws, with the body sagging downward (Fig. 2C). Since the haloperidol-plus-diazepam-treated rats did not grasp in response to either touch or traction (see Fig. 1C), how is it that the digits could hold the body up in the vertical clinging position?

When the haloperidol-plus-diazepam-treated rat was held vertically upright, the forepaw digits flexed (Fig. 3A), whereas when held vertically downward the forepaw digits extended (Fig. 3B). The flexion induced by being placed vertically upright was clearly of sufficient strength to hold the body up when the animal was placed on the horizontal

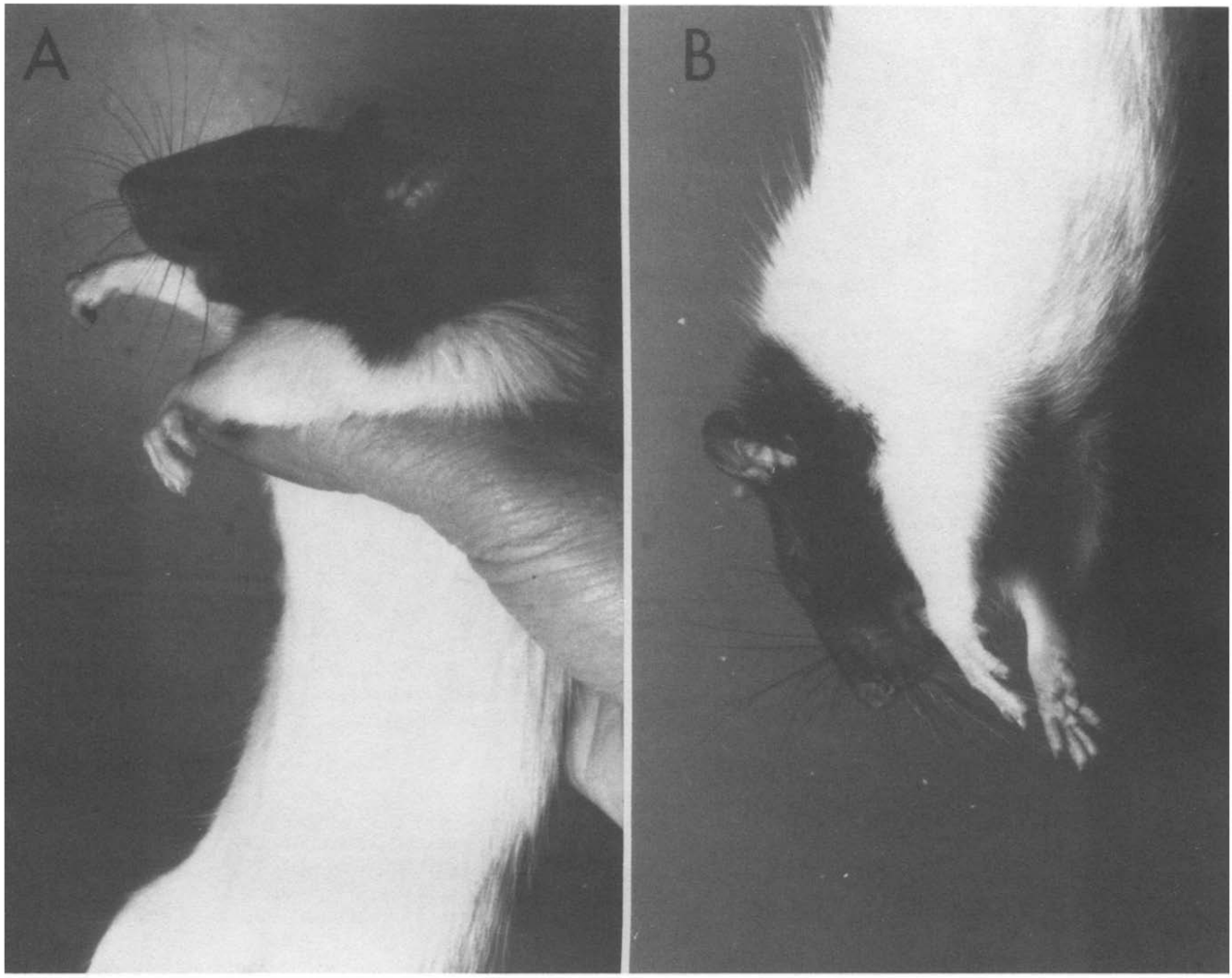

FIG. 3. When haloperidol (5 mg/kg) plus-diazepam (4 mg/kg)-treated rats are held in the air by the torso so that the head is uppermost and the body is perpendicular to the ground, the digits of the forepaws flex (A). When held upside down so that the head is bottom most, the digits extend (B). See text for further details.

clinging bars (see Fig. 2C). Such digit flexion in response to the body being in a vertical upright position must be elicited by labyrinthine stimuli, proprioceptive stimuli, or both.

Labyrinthectomy greatly diminished the strength of the forepaw digit flexion in haloperidol-plus-diazepam-treated animals, as shown by the weak grip of the rat in Fig. 4A. The photograph was taken immediately on being placed on the clinging bars, and its weaker forepaw grip can be readily compared with that in Fig. 2C. Furthermore, when the rats were held upright, less resistance was felt when the digits were pressed upward by the experimenter. Labyrinthectomy did not appear to have a comparable effect on the strength of the flexion in the digits of the hindpaws (Fig. 4A).

Bandaging the head of a haloperidol-treated rat appears to depress postural support, as indicated by the inability of the limbs to keep the animal's body off the ground while standing, and by the loss of proprioceptively mediated bracing and grasping responses of the forelimbs [11]. Based on these findings we applied a head bandage to intact haloperidol-plus-diazepam-treated rats. Like the unbandaged, labyrinthectomized, haloperidol-plus-diazepam-treated rats, they showed reduced strength of forepaw digit flexion. Like

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FIG. 4. When placed on the vertically separated horizontal clinging bars, the strength of the flexion in the forepaw digits of labyrinthectomized haloperidol-plus-diazepam-treated rat is greatly reduced, so that only the distal ends of the phalanges hold the rat upright (A). With application of a head bandage to the labyrinthectomized haloperidol-plus-diazepam-treated rat, the strength of the flexion by the forepaw digits is further reduced, so that they cannot hold the rat upright (B). With the head bandage the hindpaw digits also lose some of their strength. Application of an abdominal bandage diminishes the strength of the flexion by the hindpaws, with less effect on the forepaw digits (C). Finally, simultaneous application of both head and abdominal bandages completely abolishes all strength in the digits of both the fore and hindpaws (D).

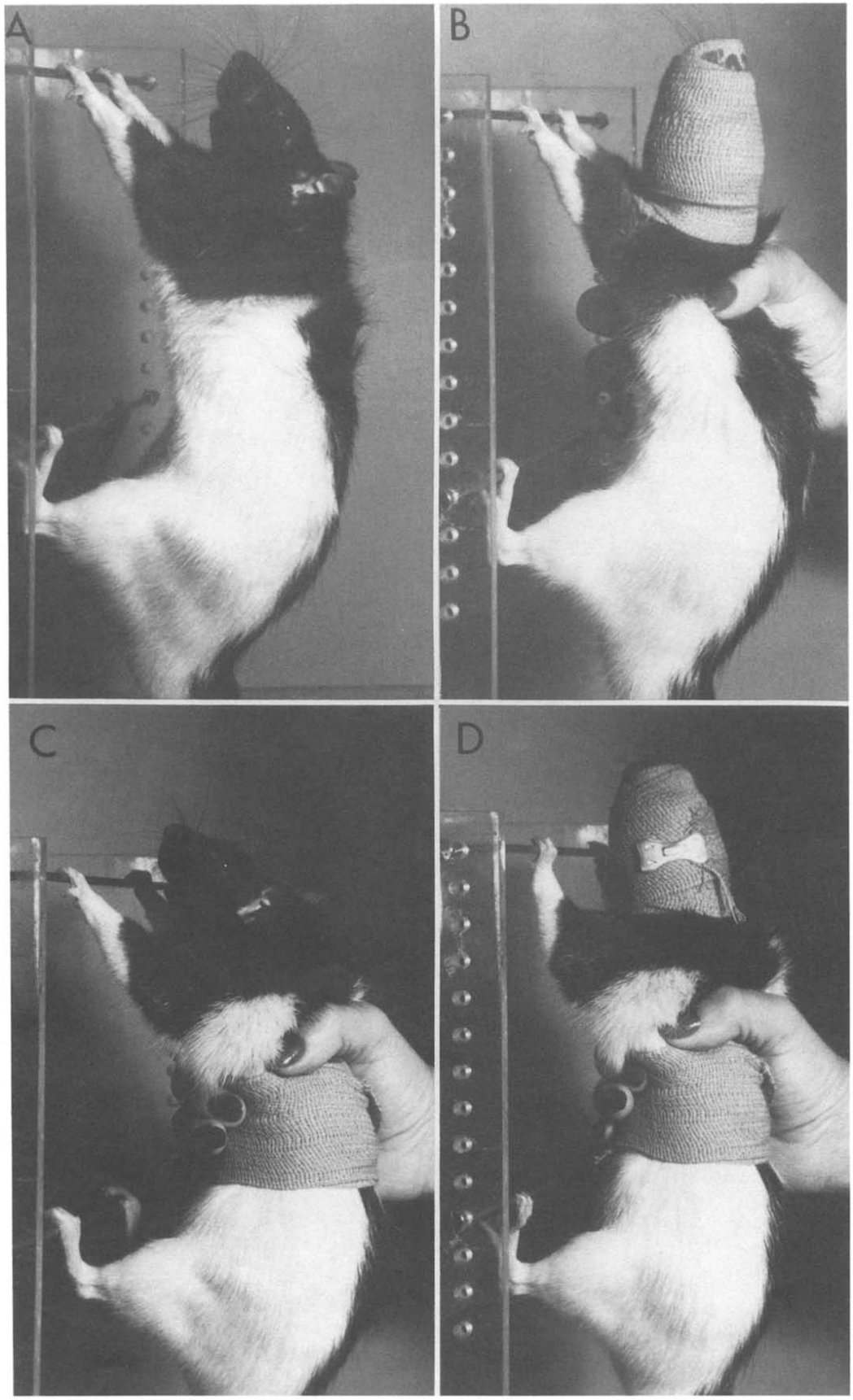

FIG. 4.

labyrinthectomy, head bandaging did not appear to affect the hindpaws. The bandage, furthermore, appeared to exert its effect on grasping directly, not indirectly due to the dorsal extension of the neck, which can be induced by the head bandage [2]. Two observations support this interpretation. Firstly, weakened forepaw digit flexion was also present when the head was not dorsiflexed. Secondly, passive neck extension in the unbandaged animal had no discernible effect on digit flexion.

Finally, application of a head bandage to labyrinthectomized haloperidol-plus-diazepam-treated rats diminished the strength of the forepaw digit flexion to the point that the forepaw digits could not hold the body up on the horizontal clinging bars at all. This is shown by the need for the experimenter's hand to hold the rat in place in Fig. 4B. However, the forepaw digits still flexed when held vertically upright; in other words, flexion in the vertical position was not abolished by labyrinthectomy and head bandaging—only the strength of the flexion was affected. Furthermore, each treatment, alone, or in combination, diminished the strength of hindpaw flexion, but less so than in the forepaws, (Fig. 4). Bandaging the abdomen of haloperidol-treated rats can abolish postural support, bracing, and grasping in the hindlimbs, while leaving these functions unaffected in the forepaws [11]. Bandaging the abdomen of either a labyrinthectomized or intact haloperidol-plus-diazepam-treated rat greatly diminished the strength of hindpaw flexion, with less effect on the forepaws (Fig. 4C). Application of both a head and an abdominal bandage completely abolished all digit flexion strength in two of the labyrinthectomized rats (Fig. 4D) and diminished it more greatly in the remaining animals than any other treatment. Taken together, these experiments suggest that grasping in fore- and hindpaws may be to some degree under separate control. In both, however, in response to being held vertically upright, flexion of the digits is elicited by a combination of labyrinthine and neck and torso proprioceptive stimuli.

Recovery of the Sensory Controls of Grasping

Over a period of 3–4 hr in haloperidol-plus-morphine, and 1–2 hr in haloperidol-plus-diazepam-treated rats, the sensory controls over grasping, initially deactivated, reappear, beginning 30 to 60 min after injection. In the former, tactile control reappears, so that gentle touching of the ventral surface of the digits and palm can elicit grasping. In the latter, proprioceptive controls reappear first, so that traction on the digits elicit grasping; later, tactile stimuli become sufficient. Therefore, both eventually recover to the point where they resemble rats treated with haloperidol alone. Visually elicited reaching and grasping only reappear after recovery from haloperidol.

It must be noted that while all rats given haloperidol displayed cataleptic behavior, and all rats given morphine in combination with haloperidol showed the deactivation of the postural support subsystem [12] and loss of tactile grasping, only about 20 percent of haloperidol-plus-diazepam-treated animals showed the complete deactivation.

DISCUSSION

Since bandaging is not a commonly used method of fractionating postural support mechanisms, some consideration ought to be given to its possible modes of action. In particular, before we can ascribe a neural role to such bandaging, other alternatives need to be considered. Firstly, application of a bandage on the head or body might act as a physical restraint, obstructing the animals' ability to move. This seems unlikely since the movements to be performed, such as flexion of the digits, are far removed from the site of application of the bandage. Secondly, the bandage may produce its effects on clinging indirectly. For example, a head bandage can induce an active dorsiflexion of the head and neck [2], which in turn induces extension of the forelimbs, and thus could account for the reduced clinging strength of the digits reported in this paper. As already discussed above, however, digit flexion is weakened by the head bandage even when the neck is not dorsiflexed. It ought to be further pointed out that the dorsiflexion of the head and neck induced by the bandage is a neural effect since denervation of the tactile sensory field of the skin of the face and scalp abolishes this effect [2,22]. Therefore, although bandaging may indeed involve physical restraint and indirect neural effects (such as described above) in some circumstances, selective neural effects on specific behaviors can be demonstrated. For example, we have recently demonstrated using bandaging of the head and abdomen, in addition to labyrinthectomy, that bracing by haloperidol-treated rats in response to horizontal displacement can be differentially deactivated in the fore- and hindquarters [11]. Furthermore, we know that bandaging has neural effects on brain function as evident in the cortical EEG shutdown produced by head or body bandaging in morphine-treated rats [4].

TABLE 1

SUMMARY OF THE SENSORY CONTROLS SUBTRACTED BY THE DIFFERENT DRUG COMBINATIONS

	Vestibular/ Proprioceptive (Body Position)	Proprioceptive (Traction on Digits)	Tactile	Visual
Haloperidol	+	+	+	+
Haloperidol Plus Morphine	+	+	−	−
Haloperidol Plus Diazpam	+	−	−	−

+ = presence; − = absence.

Table 1 summarizes the pharmacological subtraction of the sensory controls over grasping, by the use of haloperidol and haloperidol-plus morphine or haloperidol-plus-diazepam. Each drug combination subtracts more of the sensory controls over grasping, with the most simplified being haloperidol-plus-diazepam, where only vestibular, and neck and body proprioceptive controls are still operating. The sequence of recovery in the haloperidol-plus-diazepam-treated animals shows some similarity to that described for spontaneous recovery in brain damaged adult humans [16,18] and for normal human infant development [19]. For example, in development, sensory controls over grasping are sequentially added: proprioceptive stimuli in the form of traction on

the digits or arms appear first; next the fingers flex in response to tactile stimulation of the palmar surface; next a retreating tactile stimulus elicits groping and grasping [20]; and finally, visually guided grasping appears by about six months in the human infant [9]. Similarly, the haloperidol-plus-diazepam-treated rat shows that proprioceptively elicited grasping recovers before touch-elicited grasping. Visual grasping re-appears last, as the rat recovers from haloperidol.

Both Monnier [9] and Twitchell [20] report that grasping elicited by proprioceptive and tactile stimuli on the hands and feet are strengthened by proprioceptive stimuli from the neck and by vestibular stimuli. We have shown, in the haloperidol-plus-diazepam-treated rat, that digit flexion can be elicited by labyrinthine, and neck and torso proprioceptive stimuli, in isolation from tactile and proprioceptive stimuli on the paws. This head-and-body-position-elicited digit flexion is sufficient to enable the rat to cling vertically (FIG. 2C). However, the exact nature of the stimuli elicited by the body being in a vertically upright position is still unclear. Labyrinthine stimuli are obviously involved, since labyrinthectomy weakens the strength of the forepaw digits' flexion in the vertical position (Fig. 4A). Bandaging the head also weakens it, and appears to do so by acting on neck proprioceptive mechanisms. The combined effects of labyrinthectomy and head bandaging are additive, since the forepaw digit flexion of such rats is then so severely weakened that they can no longer cling vertically (Fig. 4B).

However, neither labyrinthectomy nor head bandaging, alone or in combination, abolishes the forepaw digit flexion elicited by the vertically upright posture, although they do severely weaken it. Also, these treatments appear to have a weaker effect on the flexion of the hindpaw digits (see Fig. 4). Application of an abdominal bandage severely weakens the strength of hindpaw digit flexion, affecting the forepaws less (Fig. 4C). Application of both head bandage and abdominal bandage to the labyrinthectomized rat can completely abolish all clinging by both fore and hindpaw digits (Fig. 4D). From these findings we tentatively conclude: (1) stimuli from the neck and other portions of the torso elicit digit flexion; and (2) labyrinthine stimuli are more important for the forepaws than for the hindpaws.

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