Journal of Neuroscience Methods, 36 (1991) 219–228

NSM 01196

The "staircase test": a measure of independent forelimb reaching and grasping abilities in rats

C.P. Montoya *, L.J. Campbell-Hope, K.D. Pemberton and S.B. Dunnett

Department of Experimental Psychology, University of Cambridge, Cambridge (U.K.)

(Received 16 August 1990)
(Revised version received 5 November 1990)
(Accepted 9 November 199)

Key words: Reaching tests; Motor skill; Paw use; Sensorimotor cortex; Olfactory bulb

A novel reaching test for the rat has been developed to assess the independent use of forelimbs in skilled reaching and grasping tasks. The apparatus is a plexiglas box with a removable baited double staircase. Food pellets are placed on the staircase and presented bilaterally at 7 graded stages of reaching difficulty to provide objective measures of side bias, maximum forelimb extension and grasping skill. In the present experiment, the apparatus was used to assess the reaching performance of rats following unilateral lesions of the sensorimotor cortex, unilateral lesions of the posterior cortex or bilateral lesions of the olfactory bulbs. The task has the advantage of objective over rating measurement, and the simplicity of the apparatus permits many animals to be tested concurrently.

Introduction

Studies of cortical and subcortical motor systems require sensitive tests of the functional motor capacities of animals. In rats, the need to assess goal-directed movement abilities have led to the development of a variety of tests to measure skilled paw use. These include requiring the animals to retrieve food from narrow feeding tubes (Peterson, 1934; Siegfried and Bures, 1980; Schneider and Olazabal, 1984; Pisa, 1988), from a row of narrow feeding slots (Castro, 1971; Sabol et al., 1985), from a moving conveyor belt (Evenden and Robbins, 1984) or from a food tray located at a distance outside the cage bars (Whishaw et al., 1986; Dunnett et al., 1987, 1988). In other cases, the animals have had to press levers or pressure transducers for food reward (e.g., Price and Fowler, 1981; Uguru-Okorie and Arbuthnott, 1981; Hamilton et al., 1985; Spirduso et al., 1985; Gonzalez et al., 1986; MacRae et al., 1988).

The majority of such studies have been primarily concerned either with changes in paw preference (or bias) as one aspect of an overall deficit following unilateral CNS lesions, or with a decline in overall performance following bilateral lesions. However, it is often desirable to evaluate skilled use in the contralateral and ipsilateral limbs independently. For example, only then can one evaluate the extent to which unilateral lesions produce bilateral deficits (e.g., Whishaw et al., 1986). Moreover, studies of recovery from a unilateral lesion deficit would be more sensitive if they provided independent assessment of changes in skilled use of the contralateral limb rather than measures of preference or bias to use of the ipsilateral limb.

---

* *Present address:* Cariboo College, PO Box 3010, Kamloops, British Columbia, Canada V2C 5N3.

Correspondence: S.B. Dunnett, Department of Experimental Psychology, University of Cambridge, Downing Street, Cambridge CB2 3EB, U.K.

One approach has been to restrict use of the ipsilateral limb so that the level of skill preserved in the contralateral limb can then be assessed. Peterson and Barnett (1961) bound one limb closely to the body with adhesive tape, Spriduso et al. (1985) fitted a one-arm jacket on their animals, Hamilton et al. (1985) injected local anaesthetic into the flexor muscles, and Whishaw et al. (1986) used a bracelet to prevent that paw reaching through the cage bars. An alternative strategy has been to design a test so that the configuration of the apparatus restricts the rat to use one or the other forepaw. For example, Pisa (1988) and Siegfried and Bures (1980) have used tubes arranged at the sides of the cage so that only the left paw can reach into the tube on the left side and the right paw into the right tube. However, the majority of these methods are labour intensive – measurement being based on an observer counting or rating the animals' individual reaching movements – and several require extensive training or shaping of the animals to inhibit the use of inappropriate strategies.

We have therefore sought to design a more efficient reaching test, the "staircase test", which is simple to train and which allows the collection of objective quantitative data, for the ipsilateral and contralateral paws independently, from several animals tested simultaneously. The design of the apparatus (see Fig. 1) takes advantage of the fact that rats will readily enter narrow spaces in order to gain access to food. The rats then reach down on either side of the central platform to grasp and retrieve food pellets from the steps of two descending staircases.

In order to present and evaluate the staircase test, we have used it to compare the effects of lesions of motor cortex, visual cortex and olfactory bulb on reaching performance. It is well established that motor cortex lesions affect reaching behaviour in rats (Peterson, 1934; Castro, 1971; Whishaw et al., 1986). More recently, Whishaw and Tomie (1989) have found that bulbectomy had a greater effect on reaching behaviour than did visual occlusion, suggesting that olfaction was the primary means by which rats localise food in reaching tasks. We have therefore included groups with bulbectomy and posterior cortical lesions to assess the power of the staircase test to discriminate the different impairments.

The staircase test

Apparatus

The test apparatus is illustrated in Fig. 1. The boxes are made of plexiglass 285 mm long × 90 mm high × 60 mm wide. Along two thirds of the length runs a central wooden platform with a 16.5 mm, wide trough on either side. The top surface of the platform is 27 mm wide, and overhangs the sides so as to prevent rats from simply scraping food pellets up the side of the platform. A removable double staircase is inserted into the end of the box, so as to be positioned in the troughs on either side of the central platform. Each step of the 7-step staircase contains a small 3 mm deep well into which may be placed one or more food pellets. A perspex barrier across the end wall inhibits the rat from escaping out of the end of the box. At the other end of the box, comprising the third without a platform, the floor is cut away and provides easy access for entry and removal of the rat at the beginning and end of the session. The base of the end wall is cut away to prevent the rat's tail being trapped when the box is placed back on a hard table surface.

Standard procedure

The double staircase is removed from the boxes and two 45-mg chow pellets (Custom Biological Products) are placed into each well. Food-deprived rats are placed into the test boxes through the space in the floor, the boxes are then placed gently back onto a flat table surface, and the double staircase is inserted. The standard test lasts 15 min. The staircase is removed, and the number of pellets remaining in each well on the two sides is counted, from which the total number of pellets retrieved on each side is calculated. The rat is removed and returned to its home cage. Typically, the data from each rat are combined over several days to increase the power of the standard test.

Alternative procedures

The standard test (i.e., both sides baited and tested over 15 min) provides the basic assessment

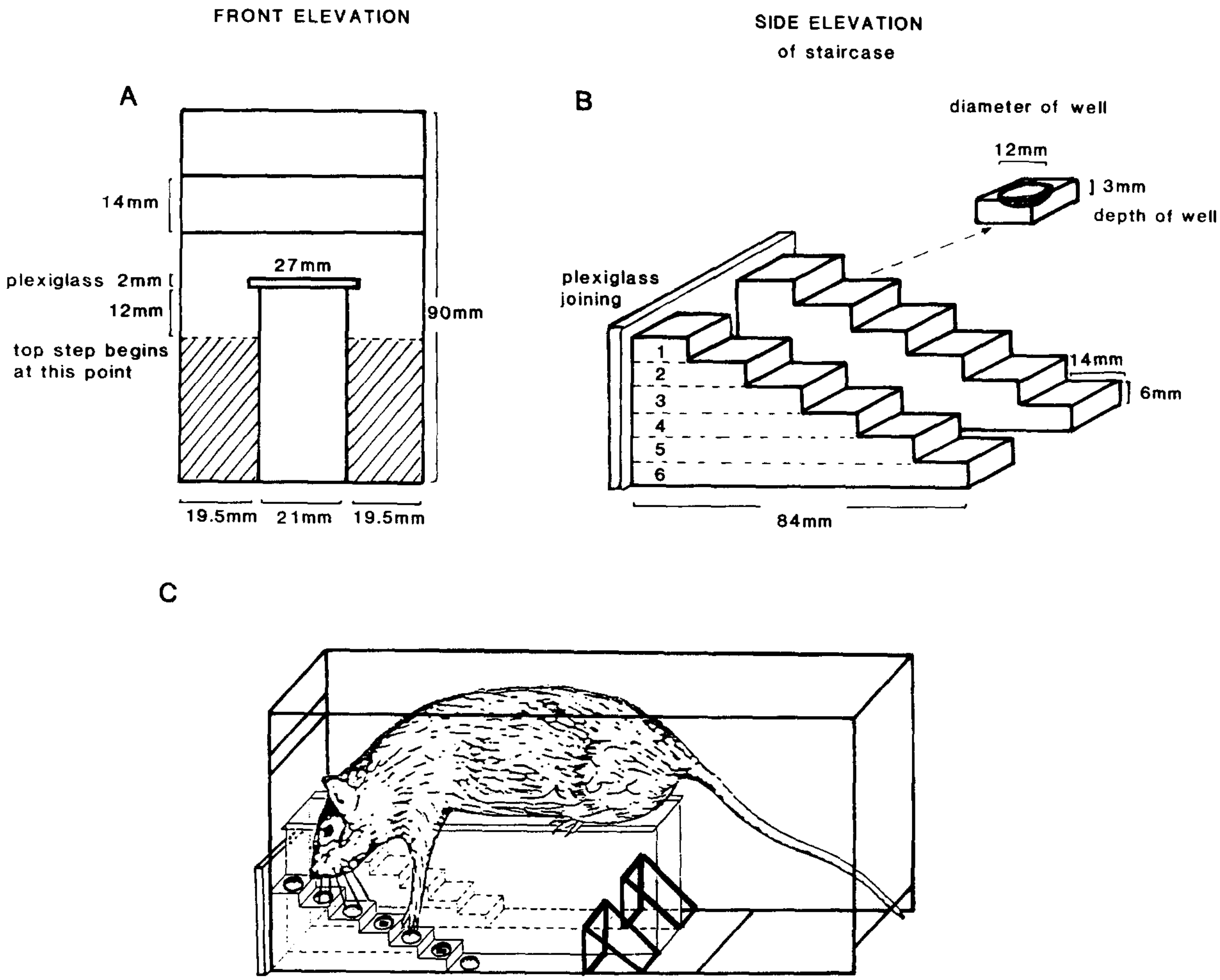

Fig. 1. The staircase test apparatus. A: Front view of the test box with the cross section dimensions of the central platform and troughs into which the staircases are inserted. B: The double staircase withdrawn for baiting. A small circular well is drilled into each step of the staircase. C. Perspective view of the test box with the staircase in position, and with a rat having climbed onto the central platform and reaching into the left staircase. The trianular blocks at the end of each trough stop pellets being flicked clear for easy retrieval from the end.

of reaching ability with the 2 paws. It is used to match animals at the outset of all experiments on the basis of levels of side bias and skill.

We have employed several variations to assess other aspects of performance:

Speed test. Both staircases are baited, and performance is recorded over 15 s, using the same measures as in the standard test. The speed test measures initial reaching preference rather than bilateral ability.

Side test. On each test, just one side of the staircase is baited. The animals receive two tests on each day, one with the left staircase baited and the other with the right staircase baited. The 2 tests are each of 5 min duration and are given in random order. Data from the two tests on each day are treated as matched pairs in the analysis, as in the standard test, in order to compare performance on the 2 sides, but tested independently. The side test evaluates whether any side difference could be attributable to the animal directing its attention or effort predominantly to one side, rather than to a greater motor skill on that side.

Methods

Subjects

Thirty young adult female rats of the Sprague–Dawley strain (OLAC, Bicester, Oxon) were used, weighing 200–250 g at the start of the experiment. Animals were housed 6 rats per cage in a colony room on a natural light-dark cycle. Food and water were available ad libitum throughout, other than during periods of behavioural testing when the rats were fed 10–15 g standard laboratory chow at the end of each day so as to maintain body weight at 90% of the free feeding level.

Behavioural tests

The present experiments were conducted in 8 identical test boxes of the design described above, with up to 8 rats tested simultaneously in each test run. Prior to surgery, animals received a single standard test to habituate them to the apparatus, by the end of which all animals reached consistently on both sides for food reward. They received three further standard tests on the following 3 days, which provided preoperative baseline levels of performance. The side on which each rat collected the most pellets during the baseline tests was designated its "preferred" side.

The animals were allocated to the 4 groups for experimental surgery, balanced on the basis of preoperative reaching scores. Unilateral motor cortex lesions were in all cases made in the hemisphere contralateral to the preferred side. In postoperative tests, the previously-preferred side is therefore referred to as the side contralateral to the lesion. To enable analysis and comparison between groups, the previously-preferred side is similarly designated as the "contralateral" side in the control rats and the rats receiving bilateral lesions.

The animals were returned to a free feeding schedule for 7 days prior to and 7 days following surgery, after which the food deprivation schedule was reinstated. The rats received a standard test on day 10 postoperatively to refamiliarise them with the apparatus. Over days 11–13 they received 3 speed tests and 3 standard tests, one of each on each day. Over days 14–16 they received 3 pairs of side tests, one on each side on each day.

Lesions

Rats were anaesthetised with 0.3 ml/100 g equithesin i.p., and placed in a stereotaxic frame with the skull surface horizontal. Lesions were conducted by aspiration through a 23-gauge stainless steel suction pipette under visual guidance. The unilateral motor and posterior cortex lesions were made in the hemisphere contralateral to the preferred paw as determined from the baseline reaching tests.

Motor cortex ($n = 9$). A unilateral bone flap was removed from 1–8 mm caudal to the frontal pole, 0–4 mm lateral to the midline and the dura parted. The surface of the fronto-parietal cortex was aspirated, over the areas of primary motor cortex (Hall and Lindholm, 1974; Donoghue and Wise, 1982), ventrally to the white matter of the corpus callosum.

Posterior cortex ($n = 9$). A unilateral bone flap was removed from 0–8 mm caudal to bregma, 0–4 mm lateral to the midline, the dura parted and the surface of the posterior parietal and occipital cortex was aspirated, to invade the visual area (Montero, 1981).

Olfactory bulb ($n = 5$). A bone flap was removed bilaterally over the olfactory bulbs, the dura was parted, and olfactory bulb tissue was aspirated ventrally to the floor of the cranium.

After each aspiration, bleeding was staunched, the wound filled with gel foam, and the skin sutured.

Controls ($n = 7$). Control animals were anaesthetised, placed into the stereotaxic frame, and removed.

Histology

At the completion of all behavioural experiments, the animals were transcardially perfused under terminal barbiturate anaesthesia with 50–100 ml saline and 250–300 ml 10% formalin. The fixed brains were viewed in a Wild macroscope, the outlines of the lesions were traced onto standard drawings of the surface of the brain, and the areas were calculated on a digitising tablet (Grafpad, British Micro, Watford, Middlesex). The brains were then sectioned at 60 μm on a freezing microtome, and every 5th section was mounted and stained with cresyl violet.

Results

One rat from each of the olfactory bulb and the visual cortex lesion groups died following surgery, and are excluded from all results. Overall performance, measured as the total number of pellets collected by each group on each side of the apparatus at each stage of the experiment, is shown in Fig. 2. More detailed analyses of performance in the baseline test and in the sides test are shown in Figs. 3 and 4, respectively.

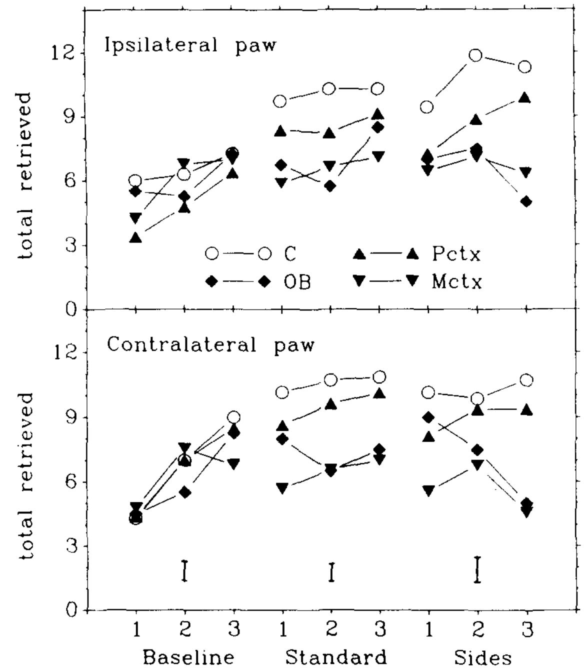

Fig. 2. Overall performance of the four groups on the ipsilateral and contralateral sides across 3 test days for each of the baseline, standard and sides tests. The vertical bars indicate 2 SEM derived from the groups × test days × side interaction of the analysis of variance for each test; the same bars apply to the ipsilateral and contralateral sides. Groups: C, sham-operated controls; OB, olfactory bulb lesions; Pctx, posterior cortex lesions; Mctx, motor cortex lesions.

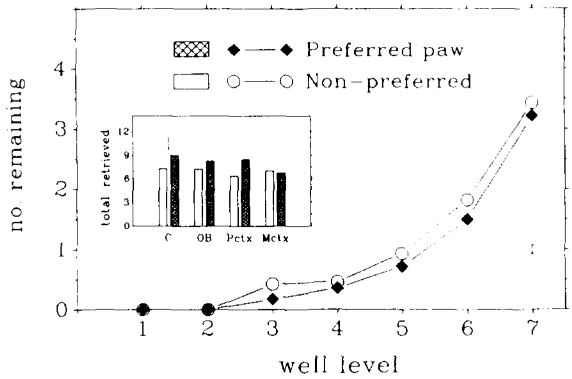

Fig. 3. Performance during baseline training. The graph indicates the mean number of pellets remaining on each step (levels 1–7) on the preferred and non-preferred sides Inset: shows the total number retrieved on the preferred side (filled columns) and non-preferred side (open columns) by each of the 4 groups on baseline day 4 prior to lesion surgery. Groups: C, sham-operated controls; OB, olfactory bulb lesions; Pctx, visual cortex lesions; Mctx, motor cortex lesions. Vertical bars indicate 2 SEM derived from the relevant interaction terms of the analyses of variance.

Baseline performance

All rats quickly acquired the basic task. Even on the first habituation test, they all climbed onto the platform, collected several pellets from the top 2 steps with the mouth or tongue and commenced reaching for pellets from lower steps on both sides of the platform. All rats continued to improve over the next 3 days of baseline training (see Fig. 2), collecting a total of 7–9 pellets on each side by the time they were matched into groups for surgery based on the day 4 performance.

The distribution of pellets remaining in each well at the end of the tests from baseline days 2–4 combined is shown in Fig. 3. The top two steps are sufficiently shallow to be within reach of the tongue at maximum extension. In the present experiment all rats were seen to quickly lick up the pellets from these two steps on each side at the start of each trial. However, even these pellets are left by trained rats not on food deprivation, and we have found that failure to remove the top pellets provides a good control for the rats' being adequately motivated.

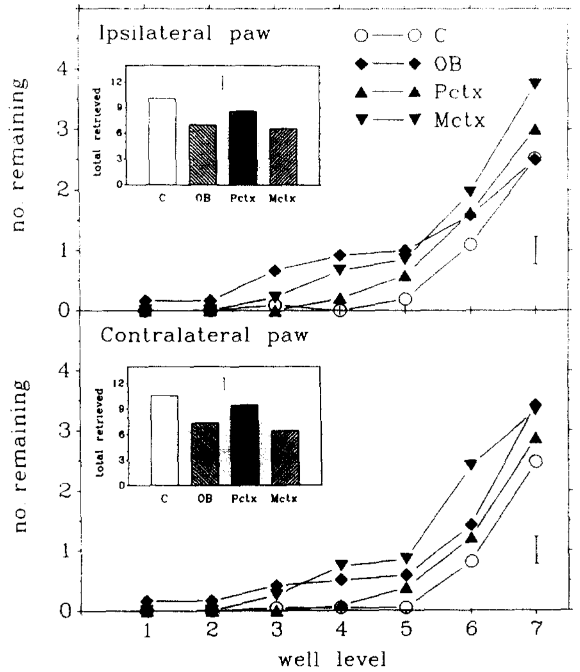

Fig. 4. Performance during the sides test. The graph indicates the mean number of pellets remaining on each step (levels 1–7) on the sides ipsilateral (above) and contralateral (below) to the lesions for the four groups. Inset: the mean number of pellets successfully retrieved (collapsed across steps) by each group on the sides test. Groups: C, sham-operated controls; OB, olfactory bulb lesions; Pctx, visual cortex lesions; Mctx, motor cortex lesions. Vertical bars indicate 2 SEM derived from the relevant interaction terms of the analyses of variance.

All steps beyond level 2 are beyond maximum tongue extension, and can only be reached with the ipsilateral forepaw. As can be seen in Fig. 3, less than 2 pellets remained at the end of the test on each of steps 3–6, which implies that the animal can reach at least to level 6. The appreciable number of pellets remaining on steps 5 and 6 suggests that the rats are not yet particularly efficient at this stage of training of the reaching task. However, the reduction of pellets on a step does not distinguish whether the pellet was successfully grasped and retrieved, or whether it was knocked off the step and down 1 or more levels. The increase of pellets to 3 or more at level 7 (see Fig. 3) indicates that at least some pellets are knocked down from higher levels to a level where they are beyond reach for retrieval. Conversely, the total number of pellets retrieved (7–9 on each side for day 4 of baseline training; Figs. 2 and 3 (inset)) provides a conservative estimate of the distance that the animal can reach to grasp and retrieve a pellet (i.e., at least to level 4 if 7 or 8 pellets are retrieved, at least to level 5 if 9 or 10 pellets are retrieved, at least to level 6 if 11 or 12 pellets are retrieved, and at least to level 7 if 13 or 14 pellets are retrieved). Although the total number of pellets collected provides the most simple and convenient measure of performance for most purposes, inspection of the pattern of pellets remaining at each level can provide further indication of the nature of the rats' performance.

Analysis of variance confirmed a highly significant difference between the different levels of the staircase ($F_{6,144} = 57.61$, $P < 0.001$). Fig. 3 is plotted in terms of the preferred and non-preferred sides for each animal, with preference defined as the side on which most pellets were collected. Consequently, the difference between the two sides is also significant ($F_{1,24} = 10.06$, $P < 0.01$). However, the magnitude of the side difference is small (see Fig. 3), indicating that normal rats do not exhibit marked side biases in their performance on the two sides. The preoperative data provided the basis for matching rats to groups (with the subsequent lesion made contralateral to the preferred side), and analysis of variance revealed no significant differences between the groups nor significant group interactions with level or side during the baseline period.

Postoperative performance

As shown in Fig. 2, the overall performance (in terms of the total number of pellets collected) of control animals continued to improve following surgery. The rats showed comparable performance on the sides tests, on which the two paws were tested independently, as on the standard test, on which the two paws were tested simultaneously. The control rats reached an asymptotic level of performance of 10–12 pellets collected on each side after approximately 1 week of training. This accords with the observation that they could just reach the 6th step, and would succeed in grasping and retrieving the pellets once trained, whereas the bottom level was beyond reach and accumulated pellets knocked down from higher levels in addition to the two placed there initially (see Fig. 4).

There was a significant difference between groups on both the standard and the sides test ($F_{3,24} = 6.03$ and 5.08, respectively, both $P < 0.01$). The difference between the 2 sides was no longer significant, nor was the group × side interaction. In each case, Dunnett's *t*-test indicated that the overall difference between groups was attributable to the motor cortex lesion and the olfactory bulb lesion groups being significantly impaired ($P < 0.05$), whereas the rats with visual cortex lesions did not differ from the controls (standard test: $t_{24} = 3.39$, 2.79 and 1.15, respectively; sides test: $t_{24} = 3.00$, 2.77, and 1.17, respectively).

The overall performance statistic (total number of pellets collected) did not differentiate the deficit in the groups with olfactory bulb and motor cortex lesions. However, clear differences become apparent when performance is analysed by levels, as illustrated for the sides test in Fig. 4. Performance on the standard test was directly comparable (not shown). The rats with olfactory bulb lesions missed an appreciable number of pellets at the higher steps (levels 1–5), within range of the tongue or easy reaching, although they did not differ from controls in the number of pellets remaining at the deepest step, collecting knocked down pellets (level 7). By contrast, the rats with motor cortex lesions did not differ from controls in collecting pellets from the higher steps (levels 1–4), but showed more misses at the longer reaches (levels 5 and 6) and more pellets knocked down (level 7). The group × level interaction was significant ($F_{18,144} = 2.70$, $P < 0.001$), and this remained significant even when the analysis was restricted to comparison of the motor cortex and olfactory bulb lesion groups alone ($F_{6,66} = 3.87$, $P < 0.002$). Again, there were no significant interactions between group and side.

A difference between the rats with olfactory bulb lesions and the other three groups was also apparent on the speed test. Within the first 15 s, rats with sham operations or either type of cortical lesion licked up the pellets from the first 2 levels and retrieved several pellets from levels 3 and 4 on either side. By contrast, the bulbectomised rats removed significantly fewer pellets from these higher levels, as confirmed by a significant group × level interaction ($F_{18,144} = 2.06$, $P < 0.01$). Again no effects of side were significant.

Histology

Following perfusion and opening of the skull, the olfactory bulbs were seen to have been effectively removed bilaterally in all rats receiving bulbectomy. No further analysis was conducted on these brains.

The brain of each rat with a cortical lesion was photographed, and the extent of the lesion was traced (see Fig. 5). The area of cortical surface damage was greater for the rats with visual cortex

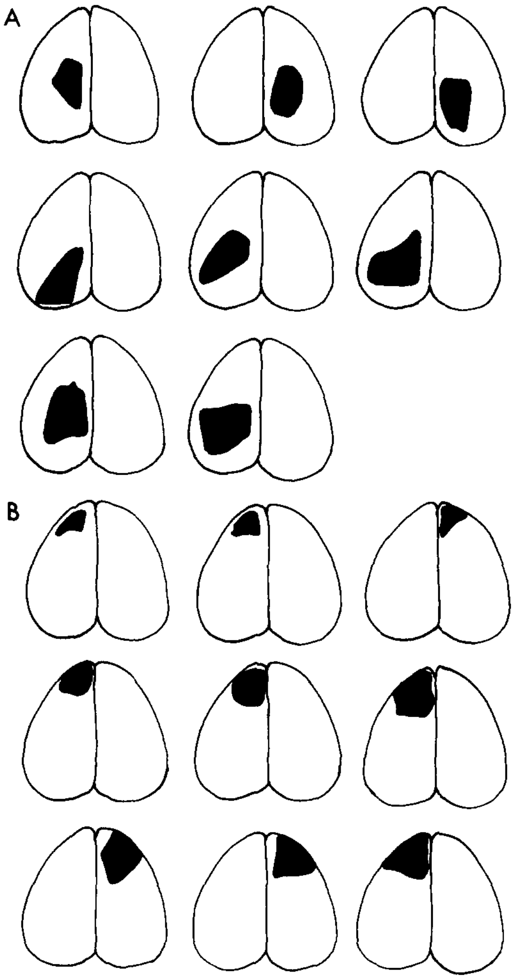

Fig. 5. Tracings of the extent of the lesions in each rat of the posterior cortex (A) and the motor cortex (B) lesion groups.

lesions than for those with motor cortex lesions (20.9 ± 1.7 mm^2 and 12.6 ± 1.9 mm^2, respectively, $t_{15} = 3.26$, $P < 0.01$).

Discussion

The staircase test has been found to be a simple and efficient test to assess paw preferences in rats and to provide quantitative measures of skilled reaching for the 2 forelimbs independently.

The collected data can be subjected to analysis at different levels of complexity, according to the requirements of the specific experimental investigation. For example, in Fig. 2 we have shown performance between groups across a range of test conditions. The overall summary statistic involving the total number of pellets collected on each of the two sides of the body is most suitable for this purpose, and can be further collapsed across repeated tests (e.g., insets in Figs. 3 and 4) to provide simple comparison between experimental treatments.

In some experimental conditions, the treatments are bilateral. Examples are provided by experiments in the development of deficits and recovery of function over time following bilateral lesions or after peripherally administered pharmacological treatments. In such circumstances the data might be further simplified by collapsing between the 2 sides. In fact, in the present experiment, although the cortical lesions were designed for unilateral influence they were found to have had predominantly bilateral effects. However, we have seen other experimental manipulations to have clearly unilateral influence on skilled paw reaching in the staircase test (Montoya et al., 1990). Consequently, the present data do not reflect a principle insensitivity of the staircase test to unilateral deficits per se, but at least in part reflect a bilateral consequence of unilateral motor cortical disturbance (see also Whishaw et al., 1986).

For other experimental purposes, a more detailed analysis of performance at each level of reach is advantageous. This is demonstrated in the present experiment by the demonstration of different patterns of deficit in the rats with olfactory bulb and motor cortex lesions (see Fig. 4). The bulbectomised rats were fully comparable to controls in their ability to grasp and retrieve pellets from the deeper steps, which may be predominantly guided by touch, whereas they were remarkably prone to miss pellets at the higher levels ("right under their noses"), which may be interpreted as a pronounced neglect of predominantly olfactory information. The rats with motor cortex lesions, by contrast, had the converse impairment. They had no difficulty in detecting and retrieving all pellets within easy reach, but were impaired in retrieving those from the deepest levels. The increase in pellets at the deepest level 7, indicates not only that less pellets were successfully grasped, but also that more pellets were contacted and knocked down out of reach, reflecting "clumsiness" or apraxia (Castro, 1971) in task performance.

The deficits in the bulbectomised group contrast markedly with the lack of significant impairment following extensive posterior cortical lesions. This latter lesion caused extensive damage in visual areas (Montero, 1981) in many animals, so that the lack of deficit supports the view that rats use a combination of olfactory and somaesthetic stimuli to guide skilled paw reaching, and make little use of visual cues (Whishaw and Tomie, 1989). This has been corroborated by finding that normal rats tested in total darkness on the staircase test perform at a similar level to rats tested in the light (C. Montoya, unpublished observations).

The major disadvantage of the staircase test is a direct consequence of its primary advantage: detailed observations of the animals' behaviour are not collected. Consequently, the advantages associated with the efficient collection of objective quantitative data must be balanced against the loss of any specific neurological evaluation of the organisation of normal behaviour and the precise nature of deficits associated with particular experimental manipulations. If the animals are not watched individually, the possibility that individual animals use unusual alternative strategies to overcome their deficits can never be completely excluded. Consequently, it is likely that in practice a combination of tests will be of greatest value in most research programmes: both observational rating of performance in this or other tests to provide a detailed evaluation of the precise motor organisation of reaching, and a simpler but more efficient test to provide data for statistical comparisons between different groups and treatments. The staircase test is ideal for this latter purpose.

A second disadvantage may be that the staircase test may not be as sensitive as other tests to forepaw preference, for example in the lack of lateralised bias induced by the motor cortex lesions in the present experiment. In particular, only the speed test and not the standard version of the test will detect relative neglect of one side when there is no loss of motor skill per se. However, the apparent lack of sensitivity to lateralised disturbance, as noted for the unilateral motor cortex lesions used here, is not a general feature of the test, since both unilateral striatal lesions and unilateral nigrostriatal lesions do induce marked contralateral deficits in the staircase test (Montoya et al., 1990).

In summary, the staircase test has several distinct advantages:

(i) The test provides objective measurement of reaching performance, rather than being dependent upon experimenter ratings of precision or accuracy.

(ii) The test requires the rats to have precise motor control over each paw in grasping and retrieving pellets, and it cannot succeed simply by scraping or scooping movements.

(iii) The rat can use its tongue to reach pellets from the first 2 steps, but no further. This provides a separate control for detecting animals which fail for lack of motivation.

(iv) The test provides separate measures of the rats' ability to use the two forepaws independently, as well as of changes of paw preference.

(v) Constraining the animal to use of just one paw is achieved without recourse to injections, jackets, bandages or bracelets.

(vi) The task requirements involve natural responses for a rat, and consequently training is rapid and simple.

(vii) The apparatus is simple to construct, and efficient to use, since several animals can be tested simultaneously. This makes it easy to design experiments with multiple trials, increasing the reliability and reducing the variance of test conditions.

The staircase test is unique in achieving these various benefits in one simple and efficient test. It is already proving its value in assessing the lateralised deficits associated with striatal lesions and recovery in response to different types of tissue transplant (Montoya et al., 1990).

References

Castro, A.J. (1972) The effects of cortical ablations on digital usage in the rat. Brain Res., 37: 173–185.

Donoghue, J.P. and Wise, S.P. (1982) The motor cortex of the rat: cytoarchitecture and microstimulation mapping. J Comp. Neurol., 212: 76–88.

Dunnett, S.B., Whishaw, I.Q., Rogers, D.C. and Jones, G.H. (1987) Dopamine-rich grafts ameliorate whole body motor asymmetry and sensory neglect but not independent skilled limb use in rats with 6-hydroxydopamine lesions. Brain Res., 415: 63–78.

Dunnett, S.B., Isacson, O., Sirinathsinghji, D.J.S., Clarke, D.J. and Björklund, A. (1988) Striatal grafts in rats with unilateral neostriatal lesions. III. Recovery from dopamine-dependent motor asymmetry and deficits in skilled paw reaching. Neuroscience, 24: 813–820.

Evenden, J.L. and Robbins, T.W. (1984) Effects of unilateral 6-hydroxydopamine lesions of the caudate-putamen on skilled forepaw use in the rat. Behav. Brain. Res.,14: 61–68.

Gonzalez, M.F., Poncelet, A., Loken, J.E. and Sharp, F.R. (1986) Quantitative measurement of interresponse times to assess forelimb motor function in rats. Behav. Brain Res., 22: 75–84.

Hall, R.D. and Lindholm, E.P. (1974) Organization of motor and somatosensory neocortex in the albino rat. Brain Res., 66: 23–38.

Hamilton, M.H., Garcia-Munoz, M. and Arbuthnott, G.W. (1985) Separation of the motor consequences from other actions of unilateral 6-hydroxydopamine lesions in the nigrostriatal neurones of rat brain. Brain Res., 348: 220–228.

MacRae, P.G., Spirduso, W.W. and Wilcox, R.E. (1988) Reaction time and nigrostriatal dopamine function: the effects of age and practice. Brain Res., 451: 139–146.

Montero, V.M. (1981) Comparative studies on the visual cortex. In C.N. Woolsey (Ed.), Cortical sensory organization, Volume 2, Multiple visual areas. Humana Press, Clifton, NJ, pp. 33–81.

Montoya, C.P., Astell, S. and Dunnett, S.B. (1990) Effects of nigral and striatal grafts on skilled forelimb use in the rat. Prog. Brain Res., 82: 459–466.

Peterson, G.M. (1934) Mechanisms of handedness in the rat. Comp. Psychol. Monogr., 9: 1–67.

Peterson, G.M. and Barnett, P.E. (1961) The cortical destruction necessary to produce a transfer of a forced-practice function. J. Comp. Physiol. Psychol., 54: 382–385.

Pisa, M. (1988) Motor functions of the striatum in the rat: critical role of the lateral region in tongue and forelimb reaching. Neuroscience, 24: 453–463.

Price, A.W. and Fowler, S.C. (1981) Deficits in contralateral and ipsilateral forepaw motor control following unilateral motor cortical ablations. Brain Res., 205: 81–90.

Sabol, K.E., Neill, D.B., Wage, S.A., Church, W. and Justice, J.B. (1985) Dopamine depletion in striatal subregion disrupts performance of a skilled motor task in the rat. Brain Res., 335: 33–43.

Schneider, J.S. and Olazabal, U.E. (1981) Behaviorally specific limb use deficits following globus pallidus lesions in rats. Brain Res., 308: 341–346.

Siegfried, B. and Bures, J. (1980) Handedness in rats: blockade of reaching behavior by unilateral 6-OHDA injections into substantia nigra and caudate nucleus. Physiol. Psychol., 8: 360–368.

Spirduso, W.W., Gilliam, P.E., Schallert, T., Upchurch, M., Vaughn, D.M. and Wilcox, R.E. (1985) Reactive capacity: a sensitive behavioral marker of movement initiation and nigrostriatal dopamine function. Brain Res., 335: 45–54.

Uguru-Okorie, D.C. and Arbuthnott, G.W. (1981) Altered paw preference after unilateral 6-hydroxydopamine injections into lateral hypothalamus. Neuropsychologia, 19: 463–467.

Whishaw, I.Q. and Tomie, J.-A. (1989) Olfaction directs skilled forelimb reaching in the rat. Behav. Brain Res., 32: 11–21.

Whishaw, I.Q., O'Connor, W.T. and Dunnett, S.B. (1986) The contributions of motor cortex, nigrostriatal dopamine and caudate-putamen to skilled forelimb use in the rat. Brain, 109: 805–843.