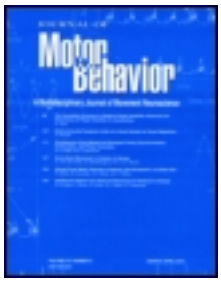

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Keeping the Body Straight in the Unconstrained Locomotion of Normal and Dopamine-Stimulant-Treated Rats

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Keeping the Body Straight in the Unconstrained Locomotion of Normal and Dopamine-Stimulant-Treated Rats

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ABSTRACT. During unconstrained locomotor behavior, rats move in and out of a straight posture of the body (including the head). In the present study, the stability of maintaining a straight body was examined in untreated rats and in rats treated with saline (SAL) or with 1 of 3 dopamine stimulants (n = 4 rats per group). The stability of maintaining a straight body can range from very high (with 0.5 mg/kg quinpirole [QUIN]), to high (first half-session with 5 mg/kg (+)-amphetamine [AMPH]), to very low (second half-session with 5 mg/kg AMPH), or can be maintained at a level similar to that observed in untreated rats (with 1.25mg/kg apomorphine [APO]). Stability was assessed by videotaping the rats and, then, by using frame-by-frame analysis, scoring the cumulative proportion of time spent in a straight posture, the frequency of transitions from one hemisphere to the other without being trapped in the midline plane, and the degree of lateral bending during turning and during walking on a curved path. The present study is one in a series identifying key variables that constrain as many degrees of freedom as possible in rat locomotor behavior. The uncovering of such variables is an indispensible step that precedes dynamic systems stability analysis and provides candidates for key variables for the modeling of motor coordination

Key words: amphetamine, apomorphine, locomotion, quinpirole, stereotypies

A major problem in the analysis of animal and human movement is whether the very many degrees of freedom composing movements can be encompassed in a low-dimensional representation on the basis of relatively few basic measures (Bernstein, 1967). The two paradigms that address this problem are coordination dynamics in the study of motor control (Kelso, 1995, Schöner & Kelso, 1988) and Eshkol–Wachman (EW) movement notation analysis in ethology (Golani, 1992).

Coordination dynamics consists of an application of dynamical systems theory and the interdisciplinary framework of synergetics (Haken, 1983). The main goal in using coordination dynamics is to develop models of motor behavior: The dynamics of collective variables or order parameters is modeled with explicit and exact motion equations, making possible predictions of the effects of perturbations or changes of control parameters. However, to simplify this modeling process and gain high-accuracy data, in this approach one uses simplified and well-controlled experimental setups with very few (or many similar) kinematic degrees of freedom, out of which order parameters can be constructed mainly according to a priori considerations (e.g., Haken, Kelso, & Bunz, 1985, Yuasa & Ito, 1990). For example, modeling of quadruped locomotion has always considered animals that walk on a straight line at a constant or continuously changed speed (Collins & Stuart, 1993; Schöner, Jiang, & Kelso, 1990; Yuasa & Ito, 1990).

In EW analysis, the articulated conceptual framework of Eshkol–Wachman (1958; Eshkol, 1980)—a symbolic movement notation—is used. Coming from an ethological tradition, producing a phenomenological description of unconstrained whole-animal movement, rather than modeling, is the main motivation for using this type of analysis. There are many possible descriptions of a behavior, each focusing on other kinematic degrees of freedom. Those descriptions that focus on the stable aspects are obviously preferable to

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those that focus on haphazard ones, not only because the sole coherent description is one that describes stable aspects but also because a kinematic stability often implies a mediating sensorimotor algorithm. Good kinematic variables are therefore those that show relative stability for extended periods of time. From an ethological, and perhaps also from a human clinical perspective, a good description should be provided in terms of few collective variables that encompass as many degrees of freedom as possible. This type of search for collective variables can, therefore, be complementary to the work in coordination dynamics.

In EW analysis, a good candidate for a collective variable is thus a quantity that reduces the apparent variability and replaces it by a relatively simple description (Golani, 1992). A good variable might offer an explanation for a large component of everything else that happens. For example, the fact that the dynamics of the vertical deviations of the head, the parts of the trunk, and the legs from an upright position can all be encompassed (and explained) by a single variable describing the maintenance of an upright posture during breathing in man suggests the existence of a mediating synergy (that has indeed been described in detail; Gurfinkel, Kots, Paltsev, & Feldman, 1971).

The search for good quantities (variables) is essentially a pattern recognition task. In such tasks, it is helpful to first use coarse filters that produce a first approximation description of the underlying structure; hence, the relatively coarse measures used in the present study. Once a collective variable is indicated, however, it can be further investigated by using both finer kinematic measures and a coordination dynamics approach (e.g., Kafkafi, Habusha, & Golani, 1996).

The present study is one in a series identifying candidate collective variables in rat locomotor behavior (such as the horizontal, forward, and vertical movement variables in Adani, Kiryati, & Golani, 1992; Eilam & Golani, 1988; and Golani, Wolgin, & Teitelbaum, 1979; Szechtman, Ornstein, Teitelbaum, & Golani, 1985).

Because of its complexity and its well-balanced nature, normal behavior does not lend itself easily to the uncovering of such variables. One way to bring them into high relief is by the study of pharmacological preparations that sometimes, if used in appropriate doses, enhance an otherwise unnoticed aspect of normal behavior.

In the present study, we examined the stability of maintaining a straight body during locomotor behavior in rats. The midsagittal (midline) plane (hereinafter called the zero plane) of the pelvis divides the vertebrate's body into two symmetrical halves when the body is in physiological position. During locomotion, this plane divides body-related space into two equal and symmetrical left and right hemispheres. Numerous studies have compared the behavior of one spatial hemisphere with that of the other (e.g., Cowey & Bozek, 1974; Denenberg, 1981; Gazzaniga & LeDoux, 1978; Glick, Jerussi, & Fleischer, 1976; Jeannerod, 1987; Kupferman, 1985; Sherman, Gabanati, Rosen, Yutzey, & Denenberg, 1980). None of these studies focused, however, on the structure of movement in and out of this plane of body-related bilateral symmetry itself.

During locomotion, the head and the chest move in and out of this zero plane (Eshkol & Wachman, 1958), sometimes staying in it and at other times crossing it without staying, on the way from one hemisphere to the other. Movement in and out of this plane is so obvious that it is almost taken for granted. Yet, whereas the zero plane is an abstract geometrical construct, the intensity of staying in it can be measured. The frequent return of the anterior parts of the trunk to this plane and the relatively long intervals of staying in it, as opposed to staying in other planes, suggests that trunk movements might be organized in reference to this plane. Before even trying to define a collective variable that behaves in a lawful way in reference to this plane, one must first examine the stability of staying in this plane. Therefore, in the present study we (a) evaluated the stability of maintaining the anterior parts of the trunk in this plane and (b) tested the hypothesis that this stability can be modified.

To evaluate the stability hypothesis, we compared the patterns of transition among the two hemispheres and the zero plane, the cumulative durations of staying in this plane and the patterns of moving out of it, in untreated, saline- (SAL) treated, and drug-treated rats. Comparison was performed in the contexts of walking, staying in place, turning in place, and progressing on curved paths. We examined five measures in each of the groups to determine how these measures behave in relation to each other. If, for example, the duration of keeping straight increases concurrently with an increase in the probability that the forequarters will be trapped in the midline upon crossing it, and if there is also a concurrent increase in the frequency of turning with a straight body (and if a decrease in one of the measures also implies a decrease in the other measures), then the notion of the stability of staying in the midline plane would be supported. By producing pharmacological preparations whose zero plane attraction is either enhanced, reduced, or both, we showed that the stability of staying in this plane can be modified.

Two of the drugs used are the prototypical stereotypy-inducing nonselective dopamine stimulants apomorphine (APO) and amphetamine (AMPH; Colpaert, Van Bever, & Leysen, 1976; Randrup & Munkvad, 1967; 1974), and the third is the dopamine agonist quinpirole (QUIN), which acts on the D2/D3 subtypes of dopamine receptors (Kebabian & Calne,1979; Nagahama, Chen, Lindheimer, & Oparil, 1986; Sokoloff, Giros, Martres, Bouthenet, & Schwartz, 1990; Waddington, Molloy, O'Boyle, & Pugh, 1990). These drugs were selected because, in preliminary observations, we were impressed by the ability of QUIN to induce walking with a straight body and turning with a straight body, and of AMPH to induce avoidance of a straight body during walking and turning.

By showing that these drugs modify the tendency to progress while maintaining a straight body (i.e., zero plane attraction), we would, except for the side benefit of adding

to the list of known effects of these drugs (e.g., Fray, Sahakian, Robbins, Koob, & Iversen, 1980; Geyer, Russo, Segal, & Kuczenski, 1987; Paulus & Geyer, 1991; Robbins, Mittelman, Obrien, & Winn, 1990), demonstrate both the stability of staying in the midline plane and the modifiability of this stability. In other words, the intensity of the tendency to maintain a straight body would account for (a) how straight the animal keeps its body while walking on a straight path; (b) how straight it is while turning in place and (c) while walking on a circular path; and (d) how often the forequarters cross, without stopping in, the midline plane.

Although this had not been our aim, the measures used provided a behavioral scale for the assessment of the effects of dopamine stimulants on behavior.

Materials and Method

Animals

Long-Evans hooded rats ($N = 22$) were selected; however, five groups, 4 in each group, were used because 2 of the 6 rats injected with QUIN were inactive during the first postinjection hour. Such inactivity has indeed been reported in a subpopulation of rats injected with QUIN and described as part of the biphasic effect of this drug (Eilam & Szechtman, 1989). Because our method can be used only with animals that walk, turn, and scan, the 2 inactive rats could not be used in the study, and our analysis was conducted on the basis of the 20 active rats. Each group included 2 males and 2 females (Department of Animal Breeding, Weizmann Institute of Science, Rehovot, Israel), weighing 250–350 g at the time of testing. They were housed in metal cages (70 × 50 × 30 cm), 2–4 rats per cage, in a colony room with lights on at 7 a.m. and off at 5 p.m. Food and water were provided ad libitum. Several days before the time of testing, the animals spent three periods of 10 min each locomoting freely in an open field (80 × 90 cm) that included several objects. Each rat was experimentally naive and was tested once.

Drugs

Our aim was to show that the stability of staying in the zero plane can be modified neurochemically and not to establish the whole spectrum of behavioral effects for each of the drugs. Therefore, a single dose of each of the drugs was administered. The (+)-amphetamine (AMPH) group was given a dose of 5 mg/kg because in earlier work (Adani, 1990; Adani, Kiryati, & Golani, 1991) this dose seemed to first enhance and then diminish the attraction of the forequarters to the midline plane. This dose is considered to be high (Russel & Phil, 1978). The quinpirole (QUIN) group was given 0.5 mg/kg LY 171555 because, on the basis of earlier experience (Eilam, Golani, & Szechtman, 1989) and preliminary screening of other doses, this dose seemed to enhance the stability of staying in the zero plane (Szechtman et al., 1985). This dose is considered to be low within the high range (Eilam & Szechtman, 1989). For the apomorphine (APO) group, because APO-treated rats showed no apparent tendency to move in relation to the midline, we chose a dose of 1.25 mg/kg in order to match the relatively high doses of the other drugs (Colpaert et al., 1976). APO was dissolved in 99% saline and 1% ascorbic acid, and AMPH and QUIN were dissolved in saline. Drugs were injected subcutaneously in the nape of the neck with a 25-gauge needle. Injection volumes were 0.1–0.15 cc per rat across drugs. Any statement describing the effect of any of these drugs pertains exclusively to the dose used. A group of 4 vehicle rats was injected with equivalent volumes of saline (SAL) and used as controls. To gain a more natural perspective, we also analyzed the behavior of a group of 4 untreated rats.

Testing Environment

The testing environment was a large flat glass platform (140 × 120 cm and 160 cm high) without walls, placed at least 70 cm away from room walls. We placed a large mirror under the platform, tilted at 45° in relation to it, to allow the videotaping of a bottom view of the rat. This view allowed an accurate evaluation of the horizontal orientation of the parts of the rat's trunk. (For the rationale for using this testing environment, see Szechtman et al., 1985).

Procedure

The animal was placed onto the center of the glass platform immediately after injection (in untreated rats, immediately after being taken out of cage) and videotaped continuously (Panasonic F-70 camera, 25 frames per second; four fluorescent lights placed below the platform lighted the rat's ventral surfaces). Untreated and SAL-treated rats belonging to the strain used in the present study became inactive and went to sleep after the first 1/2 hr, rarely moving again during the second 1/2 hr. Once again, because using our method makes sense only with animals that walk, turn, and scan, these two groups were videotaped for only the first 1/2 hr. To obtain a relatively full spectrum of drug-induced behavior with the specified doses, however, we had to video the drugged rats for a full hour (Adani et al., 1992; Eilam et al., 1989; Szechtman et al., 1985). Tests were performed during the morning hours (7–12 a.m.) in the light phase of the day-and-night cycle.

Data Acquisition

Videotapes time-coded by a Telcom Research generator (T5010) and writer (T800) were displayed on screen at a desired low speed. To allow a relatively precise assessment of the frame number at which a straight posture was established or terminated, the observer stopped the video or, if necessary, ran it back and forth. The timing of such an event (see below) was fed into the computer by using a reader (T900) and custom programs that allowed the computer keyboard to serve as an event recorder. Behavioral criteria for data acquisition were borrowed from Eshkol–Wachman

(1958; Eshkol, 1980) movement notation, a technology of description designed to express the spatial orientations and the relations and changes of relation between the parts of the vertebrate's body.

The caudocranial direction of the longitudinal axis of the rat's pelvis defines the midsagittal plane of the pelvis (termed, henceforth, the *midsagittal plane*, the *midline plane*, or the *zero plane*).

The rat's chest, head, or both might be in one of the three following states in relation to the midsagittal plane:

1. Midsagittal or zero position of the trunk: The longitudinal axes of the chest and the head are aligned in the midsagittal plane.
2. Right hemisphere: The longitudinal axes of the chest, head, or both are directed to the right of the midsagittal plane.
3. Left hemisphere: The longitudinal axes of the chest, the head, or both are directed to the left of the midsagittal plane.

Moving out of the midsagittal plane is accomplished in rats by lateral movement of the chest in relation to the pelvis, the head in relation to the chest, or both. Moving back to the midsagittal plane is accomplished by similar movements in the opposite direction (e.g., Figure 1 left, transition from bottom to top figure) or by an alignment of the chest and the pelvis in the new horizontal position acquired by the head in relation to the environment during the previous lateral movement (e.g., Figure 1 right, transition from bottom to top figure).

After staying in one hemisphere, the anterior parts of the trunk (chest, head, or both) may move continuously (i.e., without staying in the midline plane for more than one frame) to the other hemisphere or else reach the midsagittal plane and stay there. From the midsagittal plane, they may either move to the contralateral body hemisphere or move back to the hemisphere just visited. Throughout the session (continuous recording), we recorded the timing of transitions in and out of the midline plane for the head and the chest by hitting specific keys. An observer's ability to discern a straight trunk and to determine the timing of the beginning of movement out and of termination of movement in this position are rather good. Nevertheless, because our method of measurement was based on visual examination, the statement that the forequarters were in the midline plane (i.e., that the rat was straight) should be regarded as an approximation.

The following variables were examined: (a) the number of transitions among the three states, (b) the cumulative proportion of time spent in the midline plane, and (c) the frequency of continuous transitions between hemispheres. These were all calculated per 5-min bins across the session. In addition, we examined the stability of staying in the midsagittal position during two specific situations: (d) turning in place and (e) progression along curved paths.

Turning in place was examined when the pelvis changed its horizontal direction for 90° or more while the rat stayed in place with or without hind leg stepping. Three types of turns were defined, as follows, in terms of the movements that initiated the turn:

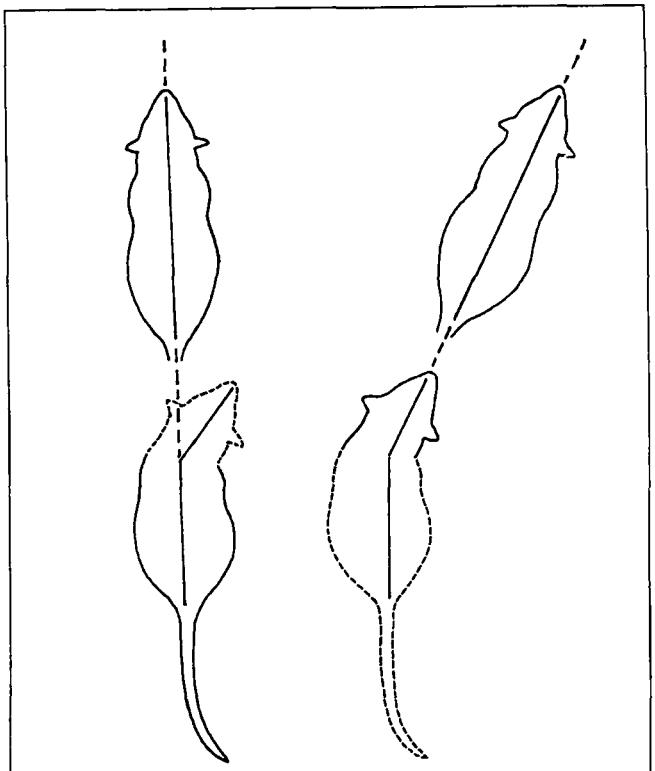

FIGURE 1. Rats align in the midsagittal plane of the pelvis either by keeping the posterior part(s) in a fixed direction in relation to the environment and then moving the anterior part(s) on the posterior parts back to the midsagittal plane (left; transition from bottom to top posture) or by keeping the anterior part(s) in a fixed direction in relation to the environment while moving the posterior part(s) so that they are aligned with the anterior part(s) (right; transition from bottom to top posture).

1. Three successive movements of the parts of the trunk in the same direction: Head moved laterally first, chest next, pelvis last.
2. Two successive movements: Head moved first, chest and pelvis moved next as one straight and rigid unit.
3. One movement of the whole trunk: Head, chest, and pelvis turned together as one straight rigid unit, aligned in the midsagittal plane.

The type of each of the turns in place that fulfilled the above criteria and occurred in the first 2 min of each 5-min bin was established and scored.

Progression on a circular path (*arc*). The path is traced in the environment by the hind legs. Only circular paths of 45° or more, including at least three successive forward steps of the "inside" hind leg were scored (when the rat changes direction, e.g., to the right, the right leg is the inside leg). Each arc was scored only once in relation to body posture, as follows:

1. A straight body (head and chest in the zero plane) was scored if during progression on the arc the rat assumed a fully straight body for at least three successive steps of the inside hind leg.

2. Of all the other arcs, a partly bent trunk was scored if, during progression on the arc for at least three successive steps of the inside hind leg, the trunk was bent into two straight parts (head bent in relation to chest, but chest kept in the zero plane in relation to pelvis; or chest bent in relation to pelvis, but head kept straight on chest).

3. In all the other arcs, the trunk was scored as comprising three segments (head bent in relation to chest and chest bent in relation to pelvis). Types of posture during progression on arcs were scored across the session (continuous recording).

Statistics

There were five treatment groups in the study: Intact (untreated controls) and SAL-, APO-, QUIN-, and AMPH-treated rats; observations were made on 4 rats in each group. For each of the rats, data about 5 variables were summarized for the first and second half of the session separately, in the following way:

1. For the number of transitions among the three states, we used the mean number per 5-min bin over half session.

2. For the percentage of continuous transitions out of all transitions, we used the percentages per 5-min bins, arcsine transformed and averaged over each half session.

3. For the time spent in the midline plane, we used the percentages of cumulative time per 5-min bins, arcsine transformed and averaged over each half session.

4. For the way in which the rat turned in place, we used the percentages of turns with a fully straight body, or partially straight body (only head bent laterally), out of all turns. With QUIN, we calculated this percentage per first 2 min of each 5-min bin, whereas with all the other treatments, because such turns were rare, we calculated their overall percentages.

5. For the way in which a rat progressed on a curved path, we have reported, because of their scarcity, the overall incidences of progressions with a straight and with a bent body.

The transformations used for the percentage of continuous transitions and for the percentage of cumulative time are commonly used, as the distribution of the transformed variable is closer to normality. Thus, for each variable, the above steps yielded two summaries for each rat: one for the first half and one for the second half of the session.

Comparisons within one treatment group between the first and the second halves of a session were done by paired t tests, that is, a one-sample t test on the differences. Comparisons between two groups as to the difference between the first and second halves was done by a two- (independent) sample t test on the differences mentioned above. Comparison between two groups in the same half-session was again done by a two-sample t test. The critical values of the t test are reported, with the appropriate degrees of freedom in parentheses.

Finally, to control for the effect of multiplicity, protecting against spurious findings in the post hoc comparisons, we used the procedure of Holm (1979) for each variable. This procedure was chosen so that we would be able to investigate the nature of interaction between part of session and group rather than only to point at its existence.

Results

Because the normal and SAL-treated groups did not differ significantly from each other in most of the measures (see section on untreated versus SAL-treated rats later in Results section), we compare in what follows drug-induced behavior only to the behavior of the SAL-treated group.

Rate of Transitions Among the Three States

One measure of the level of activity around the zero plane was provided by the rate of transitions among the three states. Both SAL- and APO-treated rats started with more than a 100 transitions per time bin, which decreased to less than half of this rate with SAL and somewhat more than half with APO (Figure 2). The difference between the first and second halves of the session was, on average, 53.42 transitions with SAL, $t(3) = 4.67$, $p < .001$, and 47.89 with APO treatment, $t(3) = 4.11$, $p < .001$. (There was no significant difference between the SAL- and the APO-treated rats: First half, $p = .4$, second half, $p = .696$.) APO-treated rats showed greater variation between the ranges of the individual rats, yet none of them had more than 200 transitions between states during any of the time periods.

QUIN-treated rats showed a uniform rate of transitions across the session, ranging between 80–200 per bin. This rate was, on average, higher than the rate observed in SAL-treated rats, especially during the second half of the session (comparison between SAL- and QUIN-treated rats: first half, $p = .017$; second half, $p < .001$). The transition rates of AMPH-treated rats at the start were not higher than those of SAL-treated rats and then rose steeply toward the end of the session to a group mean of 400 transitions per time bin (comparison between SAL- and AMPH-treated rats: first half, $p = .006$, second half, $p < .001$; the average difference between the first and second halves of the AMPH-treatment session was 228.3; $t[3] = 7.52$, $p < .001$). The phenomenon was even more pronounced in individual AMPH-treated rats; the maximal rate observed was over 700 per time bin. The AMPH-treatment-group mean attenuated the large increase in transition rates because the timing of peak transition rates differed substantially across individuals.

Continuous Transition Between Hemispheres

The attraction of the zero plane should be reflected in the percentage of direct (continuous) transitions between the hemispheres out of the total number of transitions among the three states. Random transitions among the three states

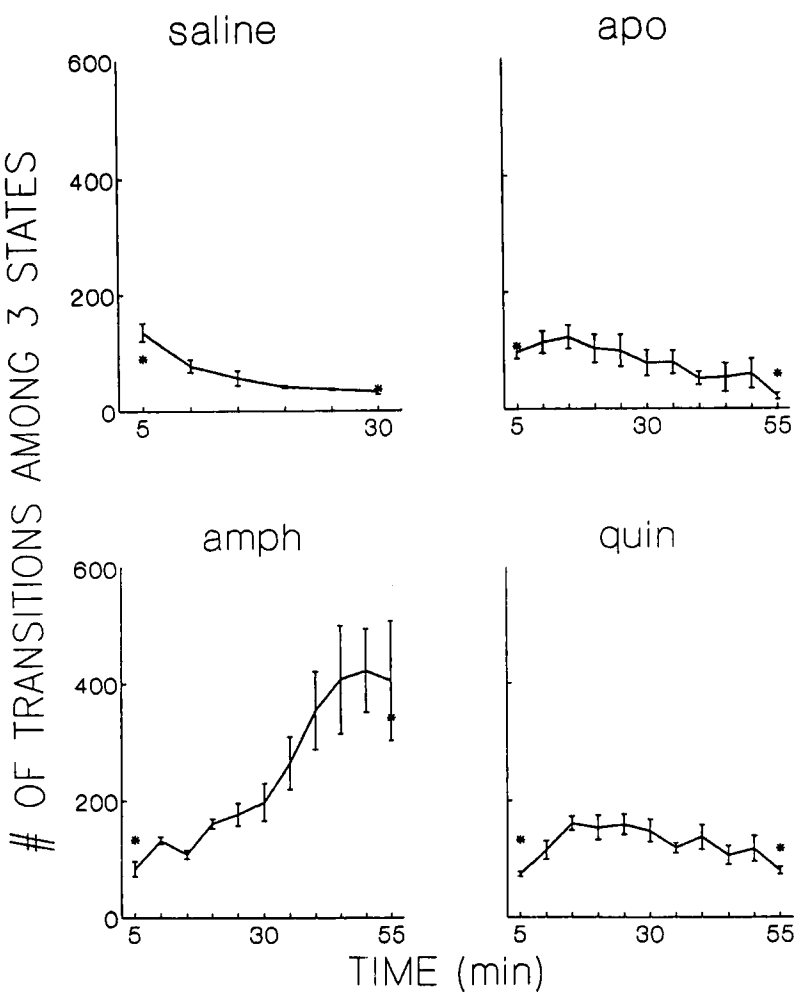

FIGURE 2. Mean frequency of transitions among the three states (zero plane, right hemisphere, left hemisphere) per 5-min bins, in each of the treatment groups. Vertical bars represent standard errors in relation to means. Asterisks represent, respectively, first and second half-session averages.

would entail a 50% rate of continuous transitions between hemispheres. An attractive zero plane should "trap" the anterior parts during crossing, thus reducing the percentage of direct transitions, and vice versa.

Stopping in the zero plane was defined as staying in this plane for more than 40 ms (one frame). With SAL, the overall percentage of continuous transitions was 4%; with APO, 5.6%; and with QUIN, as low as 1.4%. In sharp contrast, with AMPH, 20.6% of the transitions were continuous. To reveal significant tendencies across the session, we compared means per half session: Whereas with QUIN the average percentage in the second half of the session tended to decrease to less than 0.5% (average difference between the first and second halves of the session was 1.82%; $t[3] = 3.95$, $p < .001$), with AMPH the initial rate, which was around the SAL-treatment range, first decreased and then rose to more than 60% (50%–90% in individual rats; average difference between the first and second halves of the session was 34.9%, $t[3] = 5.2$, $p < .001$; Figure 3). In each of the 4 AMPH-treated rats, the steep rise was preceded by a period of 5–10 min in which the mean descended to a low of 0%–0.5%. This low and the steep increase following it are attenuated in the group graph by variation in their timing in the individual rats.

On the basis of this measure, one might conclude that the attraction of the zero plane was relatively strong in SAL-treated and APO-treated rats; it was enhanced with QUIN (comparison between SAL-treated and QUIN-treated rats: first half, $p = .009$; second half, $p < .001$) and strongly reduced with AMPH during the second half of the session

(comparison between SAL-treated and AMPH-treated rats: first half, $p = .65$, *ns*; second half, $p < .001$).

Cumulative Time of Staying in Zero Position

The relative attraction of the zero plane should also be reflected in the percentage of time spent in it. Once again, to reveal significant tendencies across the session, we compared means per half session: Rats belonging to the SAL-treated and APO-treated groups spent roughly half of the time in the zero plane (as opposed to 33% in each of the three states; comparison between SAL-treated and APO-treated rats: first half, $p = .094$, *ns*; second half, $p = .08$, *ns*).

In contrast, QUIN-treated rats showed an increasing tendency to stay in the zero plane, reaching a mean of 82.6%. (Average difference between the first and second halves of the session was 14.21%; $t[3] = 4.16$, $p < .001$.) Also, with AMPH, there was an increase in the time spent in the zero plane during the first half of the session, but this was reversed during the second half, because the mean descended to 35% (average difference between the first and second halves of the AMPH session was 27.4%; $t[3] = 3.7$, $p = .001$). Note the difference between the initial increase and subsequent decrease in the time of staying in zero, with AMPH treatment. The initial increase was similar in trend to that observed with QUIN throughout the session (Figure 4). (Comparison of SAL treatment with QUIN treatment: first half, $p = .006$, second half, $p < .001$. SAL with AMPH: first half, $p = .032$, second half, $p = .135$, *ns*. QUIN with AMPH: first half, $p = .538$, *ns*; second half, $p < .001$.) Using our regular testing method, the difference between the SAL- and the AMPH-treatment groups' second halves was not significant statistically because the AMPH group started from a higher level and monotonically decreased to a much lower level than that of the SAL-treated group. Thus,

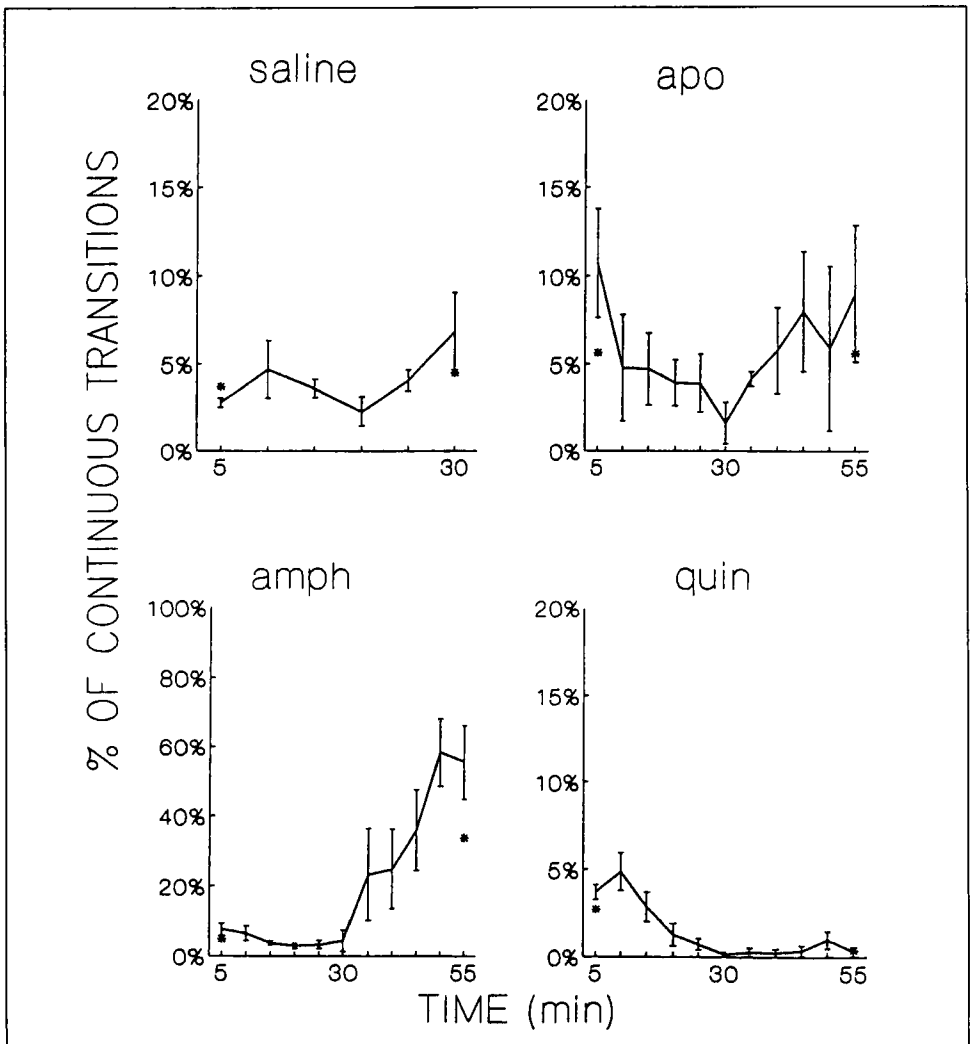

FIGURE 3. Mean percentages of direct transitions between hemispheres, per 5-min bins across the session, in each of the treatment groups. Vertical bars represent standard errors. Asterisks represent, respectively, first and second half-session averages. Note that a different *y*-axis scale has been used for amphetamine-treated rats.

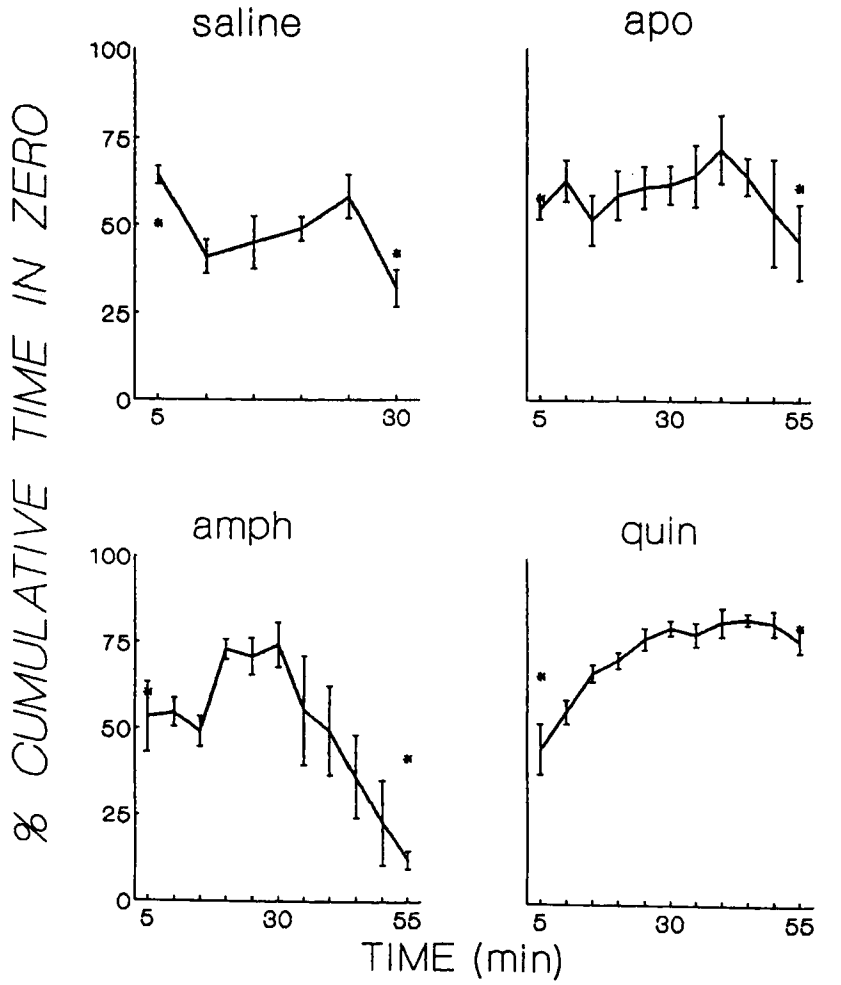

FIGURE 4. Percentage of cumulative time of staying in the zero plane per 5-min bins across the session in each of the treatment groups. Vertical bars represent standard errors. Asterisks represent, respectively, first and second half-session averages.

in the last 5 min, the AMPH-treated rats' mean amounted to about one third of the SAL-treated-rats' mean.

The dynamics of cumulative time in the zero plane could be a mere by-product of the different modes of locomotion observed with AMPH and QUIN treatment. For example, long bouts of forward locomotion during parts of the session could have resulted in increased time in zero, whereas staying in place with side-to-side forequarter movements could have resulted in decreased time in zero. Figure 5 refutes this hypothesis for QUIN. With this drug, the rats alternated, throughout the session, between forward progression and staying in place (Eilam, Golani, & Szechtman, 1989). Figure 5 presents time in zero only during intervals of staying in place, however. As can be seen, time in zero increased across the session in spite of the fact that the rats stayed in place (Figure 5; average difference between the first and second halves of the session was 9.74%, $t[3] = -3.595$, $p = .018$).

A similar examination was not possible in the case of AMPH treatment because, in the strain of rats used here, staying in place disappeared during a large part of the session (Adani, 1990). Therefore, we had to examine time in the zero plane, for each of the rats, in parallel with a record of its mode of locomotion at that time. With 5 mg/kg AMPH, rats showed in the course of the session a stage in which they alternated between walking, staying in place, and turning in place (Stage I in Figure 6), a stage of relatively pure forward progression (Stage II in Figure 6), a stage of staying in place with relatively pure side-to-side forequarter movements (Stage IV in Figure 6), and a stage consisting of both extensive forward progression and simultaneous side-to-side movements (Stage III; Adani et al., 1992). Figure 6 refutes the hypothesis that time in zero is a by-product of the mode of locomotion by showing that (a) pure forward progression (Stage II) does not imply increased time in zero (rats 2 and 4), (b) extensive forward

progression (Stage III) can be associated with decreasing time in zero (all 4 rats), and (c) staying in place (Stage IV) does not imply decreasing time in zero (rats 1 and 3).

Turning in Place

Turning in place is an obvious locomotor context in which rats might leave the midsagittal plane. Turning by lateral bending of the head (on the chest) and the chest (on the pelvis) was present in all groups and constituted the vast majority with SAL, APO, and AMPH treatment. As can be seen (Figure 7), turning with chest in the zero plane (only head bent laterally) was relatively rare in SAL-, APO-, and AMPH-treated rats. Its relative frequency increased, however, across the QUIN-treatment session. Furthermore, turning with a fully straight body was observed only with QUIN. The percentage of turns with a relatively or completely straight body amounted to an overall percentage of 30% and increased in the course of the QUIN session, reaching a peak of more than 50% per time bin. This measure thus supports the conclusion that QUIN enhances the attraction of both the head and the chest to the midsagittal plane.

Progression on Arcs

Locomotion on curved paths was rare in all the examined groups (the highest frequency of three arcs per 2-min interval was observed in a QUIN-treated rat who performed during the same interval 46 turns in place consisting of 45° or more). Nevertheless, the kinematics of progression on arcs provides an additional measure of zero plane attraction. Because the overall numbers of arcs performed by individual rats were small in all groups, data were pooled separately for fully straight and laterally bent trunks for each of the groups. As is shown in Table 1, whereas SAL-treated and APO-treated rats never walked on an arc with a fully straight body for three successive steps, AMPH-treated rats performed 4% (1 out of 23), and QUIN-treated rats 30% (56 out of 181) of such arcs while keeping their chest and head in the zero plane. This measure thus also supports the conclusion that QUIN enhances the attraction of the zero plane.

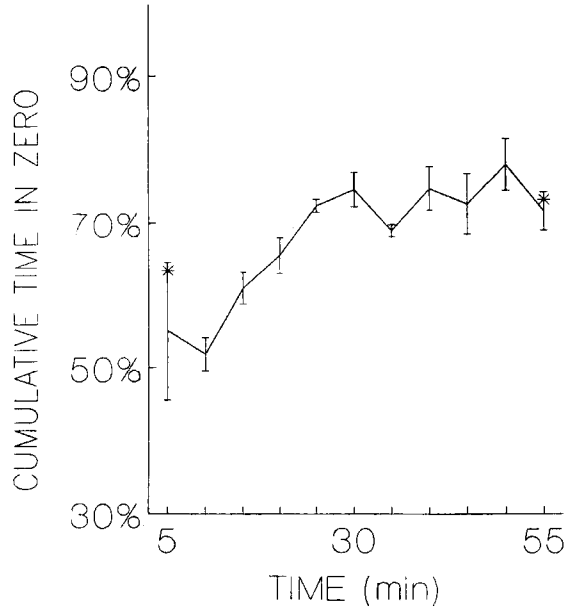

FIGURE 5. Percentage of cumulative time of staying in the zero plane per 5-min bins, during periods in which the QUIN-treated rats stayed in place, across the session. Vertical bars represent standard errors. Asterisks represent, respectively, first and second half-session averages.

Untreated Versus SAL-Treated Rats

To relate the results to untreated rats' behavior, we compared the SAL-treated rats' means per half-session to the respective means obtained in untreated rats. The differences were not significant in two of the measures (total number of transitions and cumulative time in the zero plane). The differences in direct transitions between hemispheres were significant and amounted in both halves of the session to 6% in the untreated and 4% in the SAL-treated rats ($p < .05$ in the first half). Turning in place with chest (but not head) in zero, amounted to 1.39% in the untreated and 6.7% in the SAL-treated rats, both very small compared with the QUIN-treated rats (see Figure 7). It may be concluded, therefore, that the strength of zero plane attraction was similar in range in untreated and SAL-treated rats.

Discussion

Methodological Considerations

We were motivated to perform this study by the observation that drug-induced behavior sometimes enhances aspects of the organization of behavior that are less conspicuous in normal conditions: If the stability of maintaining a straight body (including the head) can be modified by drugs, then this stability might also play a role in the organization of normal behavior. This strategy, of proceeding from pathological to normal behavior, proved useful in the past in first revealing the rules of transition out of immobility in lateral-hypothalamus-lesioned rats (Golani et al., 1979) and then enabling us to use these rules as a "search image" in the study of ontogeny (Eilam & Golani, 1988), drug-induced behavior (Szechtman et al., 1985), and a variety of contexts and species (Golani, 1992).

Our aim in this study has been to show that keeping the body straight can be a stable behavior and to examine the modifiability of this stability. The movement of the untreated and SAL-treated rats in reference to the midline plane can be better appreciated once it is contrasted with that of the drug-treated groups. As was evidenced by four relatively independent measures, one group of drug-treated rats could not be distinguished from normals, another actively avoided keeping the chest and head in the midline plane at

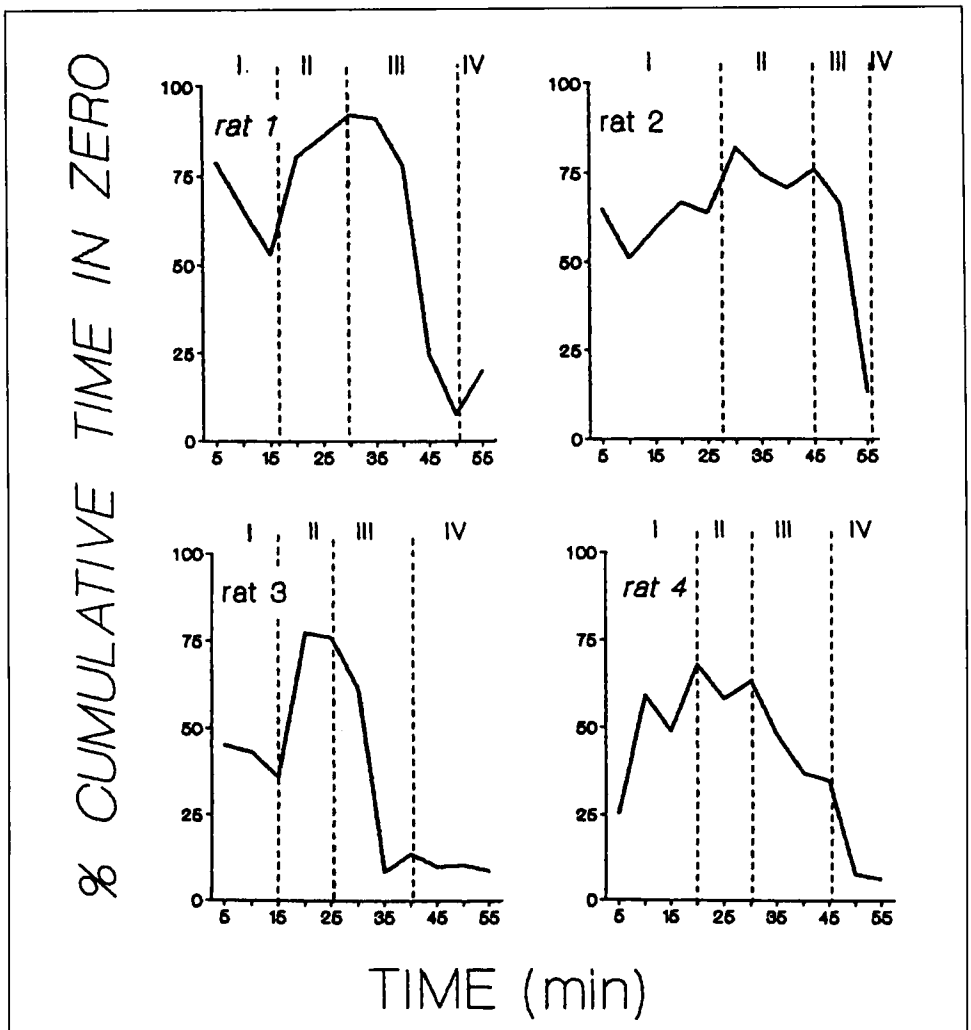

FIGURE 6. Mean percentage of cumulative time of staying in the zero plane per 5-min intervals in individual rats treated with amphetamine, in relation to the four locomotor stages that partitioned the amphetamine treated rats' session (Adani et al., 1991). Vertical interrupted lines represent boundaries between stages. Stage I: periods of activity and arrest. Stage II: forward progression. Stage III: forward progression with rhythmic side-to-side horizontal forequarter movements. Stage IV: absence of forward progression.

a particular stage of drug action, and a third kept these parts excessively in this plane. By showing that the behavior observed in the normal animal is an intermediate one, we have supported the notion that keeping the body straight is a stable and modifiable behavior.

Had our aim in this study been to describe the full spectrum of effects of each of the three drugs on behavior, we would have had to obtain dose–response curves for each of the drugs on each of the measures. But merely for the demonstration of the modifiability of zero plane attraction, a single dose proved sufficient.

Three Profiles of Behavior

Untreated and SAL-treated rats kept their forequarters in the zero plane for roughly half of the time; their forequarters got trapped in this plane in the vast majority of cases, upon reaching it (94%, untreated; and 96% with SAL treatment), and they did not turn in place and did not walk on an arc without bending their head or forequarters laterally.

With 5 mg/kg AMPH, the normal level of cumulative time of staying in the zero plane was increased in the course of the first half-session but strongly reduced in the second half of the session. The rate of getting trapped in the midline plane was first increased (to 99.5%–100% in each of the rats) and then reduced to a mean of less than 40%. These rats turned in place by lateral bending of head and chest, and never with a fully straight body. They did perform, however, 6.7% of the examined arcs with a straight body.

Unlike AMPH's biphasic effect, 0.5 mg/kg QUIN enhanced only the normal level of zero plane attraction by increasing the cumulative time of staying in the zero plane to 82.5%, the rate of trapping of the anterior parts to more than

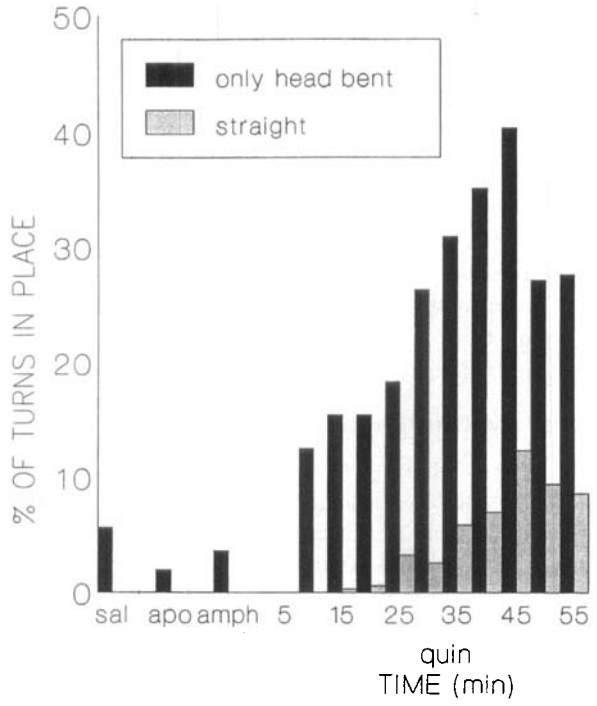

FIGURE 7. The percentages of types of turning in place per 5-min bins across the session in rats treated with quinpirole, and the overall percentages of such turns in rats treated with saline, apomorphine, or amphetamine.

99.5%, the frequency of turning in place with a straight chest to 40%, and with a fully straight body to 10%, and by increasing the percentage of progressions on arcs with a fully straight body to 30%. The tendency to turn in place with a straight body has also been demonstrated in infant rats with 0.5 mg/kg QUIN (Eilam, Szechtman, & Spear, 1992).

The increase in stability observed with both drugs during the first half of the session was maintained during the second half of the session with QUIN and reversed with AMPH. It is as though AMPH induced a milder form of QUIN-type behavior during the first half-session, before inducing the opposite effect. This opposite effect of periodic movements around the zero plane has been ascribed to the serotonergic (5-hydroxytryptamine [5-HT]) syndrome elicited at 5 mg/kg AMPH (Ernst, 1967, 1969; Kuczenski & Segal, 1988 Taylor, Goudie, Mortimer, & Wheeler, 1974).

In contrast to the pronounced effects established for QUIN and AMPH, APO had no discernible effect on the stability of the forequarters in the midline plane. The results obtained with this drug show that rats may be highly hyperactive and stereotyped and yet show no change in the level of stability of staying in the midline plane.

Does Zero Plane Stability Suggest a "Good" Variable?

A single phenomenon, the stability of maintaining the forequarters in the zero plane, constrains (and in this sense also explains the behavior of) several variables, including the amount of time spent in the midline, the smoothness of transition between the hemispheres, the way in which a rat turns in place, and the way in which it turns while walking. It also differentiates between the apparently similar effects of three dopamine stimulants on behavior. Once pointed out, the phenomenon is so robust that the differences are almost self-evident and easy to score. Yet, as with any candidate for a key variable, one can never be sure that the observed regularity in its dynamics is not merely a reflection of another related but more relevant variable. For example, one must distinguish between the movements of the chest in relation to the midsaggital plane of the pelvis and of the head in relation to the midsaggital plane of the chest; also, it might be worthwhile to examine the movements of each of the caudal segments in reference to their respective rostral neighbor.

The strength of zero plane stability was not a mere reflection of the rats' level of activity, because hyperactivity was a common denominator with APO, AMPH, and QUIN, and yet each shows a different profile of attraction. Conversely, similar levels of stability were scored during moderate activity (first half-sessions in untreated and SAL-treated rats), very low activity (second half-sessions in untreated and SAL-treated rats), and hyperactivity (with APO).

Similarly, the strength of attraction was not merely a reflection of enhanced forward locomotion, because during periods of such locomotion, APO-, AMPH-, and QUIN-treated rats showed distinctly different levels of zero plane stability.

The level of stability was not merely a reflection of the abundance of side-to-side forequarter movements, because during periods of staying in place with enhanced side-to-side forequarter movements, APO-, QUIN-, and AMPH-treated rats showed distinctly different levels of stability in zero. Still, the exceptionally high rate of side-to-side movements observed during the second half of the AMPH-treatment session (up to two transitions between states per second) could have made stopping at zero difficult. In

TABLE 1
Incidence of Observations Across the Section (No Sampling) of Rats in Each Treatment Group Walking With a Straight or a Laterally Bent Trunk In a Curved Path (Arc)

	Treatment group			
	SAL	APO	AMPH	QUIN
Straight trunk	0	0	1	56
Bent trunk	22	128	22	125

Note. SAL, APO, AMPH, and QUIN treated groups were administered, respectively, saline, apomorphine, amphetamine, or quinpirole.

other words, it could be that the rat failed to stop at zero because of the high rate (and therefore high velocity) of performance. This hypothesis can be tested by examining the head's angular velocity throughout the head's side-to-side cycle: Whereas slowing down upon approaching the midline plane would support the hypothesis by revealing the existence of a point attractor at zero, speeding up toward and across this plane would refute it by revealing that the static point attractor has been transformed into a periodic limit-cycle attractor. A recent examination of the velocity trajectory supported the second, bifurcation to a limit cycle, hypothesis (Kafkafi & Golani, unpublished data). The pronounced periodicity of the side-to-side forequarter movements (Kafkafi et al., 1996) further supported this hypothesis. With all three drugs, neither ataxia nor loss of balance has been observed. Differences in attraction could not be attributed, therefore, to these factors. Furthermore, each of the profiles of attraction corresponded to a specific, highly characteristic pattern of coordinated locomotion (Adani et al., 1992; Eilam et al., 1992; Kafkafi et al., 1996; Szechtman et al., 1985). Because each of the locomotor patterns could presumably be characterized by a respective pattern of torques, it could be argued that different patterns of torques could explain different patterns of attraction. On the other hand, the essence of the synergetic argument (Bernstein, 1967) is that motor coordination cannot be fully explained by biomechanical constraints and must be supplemented by a computational explanation: A reduction of the excessive number of mechanical degrees of freedom available to the organism is achieved through the use of a small number of coordinative structures. (A coordinative structure or synergy consists of a group of muscles spanning several joints, and capable of contracting independently of each other. The muscles become functionally linked so that they behave as a single task-specific unit; Turvey, 1990.) The results of the present study may mean that a single coordinative structure produces the different locomotor patterns by increasing only zero plane attraction (QUIN) or by first increasing it (first half-session of AMPH) and then replacing the static equilibrium point with a periodic equilibrium cycle (second half of AMPH session).

The Expression of Zero Plane Stability in Moment-to-Moment Behavior

Once pointed out by Eshkol–Wachman movement notation analysis, the stability of staying in the zero plane can readily be discerned in direct observation. Untreated rats' spontaneous locomotor behavior typically consists of an alternation between bouts of forward progression and periods of stopping and staying in place (Eilam & Golani, 1989, 1990; Golani, Benjamini, & Eilam, 1993). The anterior parts of the trunk move out of the zero plane in only two contexts: during staying in place or during a change in the horizontal direction of progression. During forward locomotion, a movement of an anterior part(s) out of zero implies subsequent straightening by alignment of the caudal part(s) in the new spatial direction of the anterior part(s). These regularities also characterized the SAL-, APO-, and QUIN-treated rats. The last group, however, tended to turn with a straight, or almost straight, body. In contrast, with AMPH, during the stage in which horizontal movement was superimposed on forward progression (third stage in Adani et al., 1992) rats kept moving the anterior part(s) out of zero while the posterior parts progressed forward, maintaining all the while their original spatial direction. It is during this stage that the anterior parts crossed the zero plane from side to side, without stopping there, in increasing frequency.

Competition Between Response Categories

The Lyon-Robbins hypothesis (1975) suggests that a rat's behavioral repertoire becomes restricted in the course of AMPH activation as a result of competition between response categories. Initially, AMPH-induced behavioral activation permits complex behavioral sequences, including several response types. As the hyperactivity induced by AMPH is increased and the time required for the completion of response categories is reduced, responses start to compete with each other, ultimately eliminating some of the response categories from the rat's repertoire. This results in the substitution of locomotion and rearing with so-called stereotypies. Although the bases for the Lyon-Robbins hypothesis were observations at the macro level of whole behavioral sequences, movement notation analysis gives one an opportunity to examine its validity at the micro level of movements of the parts of the body. A previous study has shown that with APO treatment, vertical movement is eliminated first and forward movement next, leaving a residue of horizontal movement (Szechtman et al., 1985). Another version of this process has been described with AMPH treatment (Adani et al., 1992; Eilam, 1987; Golani, 1992). Could this process of spatial shutdown be attributed to a competition between the vertical, forward, and horizontal spatial component-variables? With 0.5 mg/kg QUIN, all the three spatial variables were enhanced but nevertheless coexisted (Eilam et al., 1989), even with chronic treatment (Eilam et al., 1992; Einat & Szechtman, 1993). Therefore, if these spatial variables are taken to represent at the micro level the macro response categories of the Lyon-Robbins hypothesis, then the hypothesis does not apply in the case of QUIN-induced behavior. But the QUIN preparation does not refute the hypothesis; it shows merely that hyperactivity within each of the spatial variables is not sufficient for their mutual occlusion. On the other hand, the enhancement of the three spatial variables was accompanied, under QUIN, by a concurrent restriction, documented in the present study, of horizontal movement in body-related space (restriction of lateral bending). This means only that competition among the three variables, if present, might change the form of movements in body-related space, without causing mutual occlusion in absolute space.

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