# Differential effects of spinal transection on sympathetic nerve activities in rats

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# Differential effects of spinal transection on sympathetic nerve activities in rats

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TAYLOR, ROBERT F., AND LAWRENCE P. SCHRAMM. *Differential effects of spinal transection on sympathetic nerve activities in rats.* Am. J. Physiol. 253 (Regulatory Integrative Comp. Physiol. 22): R611–R618, 1987.—We measured renal, splenogastric, and lumbar multiunit sympathetic activities in chloralose-anesthetized, paralyzed, and artificially respired Sprague-Dawley rats. Acute spinal transection reduced arterial pressure and lumbar sympathetic activity. However, renal and splenogastric activities were doubled after transection. We conclude that spinal systems exist in the rat that are capable of maintaining renal and splenogastric, but not lumbar, sympathetic activities after spinal transection. Cross-correlation and power spectral analysis of simultaneously recorded sympathetic activities indicated that renal and splenogastric activities often, but not always, shared periodicities near the respiratory rate. These shared periodicities were responsible for high correlations between renal and splenogastric activities. After spinal transection, the shared periodicities usually disappeared, and correlations were reduced. Renal and lumbar activities were rarely strongly correlated, and they rarely shared major periodicities. We conclude that brain stem systems often provide synchronization of abdominal sympathetic activities. However, these activities can be independently generated in both intact and spinally transected rats.

cardiovascular regulation; bulbospinal; cross-correlation; spectral density; renal nerve; lumbar sympathetic activity; splenic nerve

TO WHAT EXTENT is supraspinal drive necessary for maintenance of sympathetic activity? Spinal transection decreases arterial pressure in both humans and experimental animals (see Ref. 19 for review). This observation has led to the impression that spinal transection decreases the activity in all sympathetic nerves. Indeed, investigators have reported reduced efferent activity in individual sympathetic nerves after spinal cord transection in humans (22) and experimental animals (2, 4, 12, 16).

However, spinal transection does not reduce sympathetic activity to similar degrees in all nerves, and transection may even increase activity in some. Acute spinal transection in cats reduces renal, but not splenic, sympathetic activity (16). In $\alpha$-chloralose-anesthetized rats, renal nerve sympathetic activity approximately doubles after spinal transection (17, 21). In fact, the gastric hypomotility that follows spinal transection in humans has been attributed to elevated gastric sympathetic activity (8). These observations suggest that spinal transection may differentially affect levels of activity in sympathetic nerves because spinal systems alone can generate substantial sympathetic activity destined for only certain tissues. The rat is an excellent animal in which to study the effects of spinal transection on the distribution of sympathetic activity, for spinal systems appear to be very active even minutes after transection.

*How Does Spinal Transection Alter Synchronization of Sympathetic Discharges?*

Supraspinal systems are known to affect the synchronization of sympathetic activity in a number of ways. First, brain stem respiratory systems often modulate sympathetic activity at the respiratory rate (1). Second, baroreceptor afferents synchronize activity in many sympathetic nerves to the cardiac cycle (4). Finally, in cats, intrinsic brain stem generators impose a three- to six-cycle rhythmicity on sympathetic activity (10).

Given the existence of multiple brain stem systems which synchronize sympathetic activity, spinal transection should reduce similarities between the activities in different sympathetic nerves. Indeed, Gootman and Cohen (11) found that spinal transection reduced the $\rho$ values of cross-correlations computed between splanchnic and cervical sympathetic nerve activities in cats, and Ardell et al. (3) found that transection similarly affected correlations between the external carotid and renal nerves. However, all previous studies of the effects of spinal transection on sympathetic synchronization have been conducted in preparations in which transection decreased sympathetic activity. Ours are the first observations on the synchrony of nerve activities, some of which were increased by spinal transection.

## METHODS

*Surgical methods.* Male Sprague-Dawley rats (Charles River), weighing between 200 and 300 g, were anesthetized with ether followed by $\alpha$-chloralose (100 mg/kg iv). When necessary, additional doses of $\alpha$-chloralose (25 mg/kg) were administered via a femoral venous cannula. A cannula was placed in the right carotid artery for the measurement of arterial blood pressure. Rats were artificially ventilated through a tracheal cannula after being paralyzed with gallamine triethiodide (Flaxedil, 30 mg/kg). A servo-controlled heating pad maintained body temperature between 36 and 37°C throughout the experiment.

Through a ventral midline laparotomy, the left ileolumbar artery and vein were ligated, sectioned, and retracted. This retraction deflected the descending aorta and exposed the lumbar sympathetic chain, which was carefully dissected and marked with a loose loop of suture. This marker was used later to locate the lumbar sympathetic chain via a dorsolateral incision. The ventral incision was securely sutured, and the rat was placed in a stereotaxic frame with its lower torso positioned on its right side. The spinal cord was exposed via a laminectomy from cervical levels $C_1$ to $C_6$. Once the dura was removed, the exposed spinal cord was kept moist with warm mineral oil in preparation for transection. The spinal cord was completely transected at $C_1$ with a scalpel blade and a fine suction tip. The completeness of the transection was confirmed at the end of each experiment by dissection of the site of the lesion.

### *Nerve Recording and Signal Processing*

The renal, splenogastric, and lumbar sympathetic nerves were all approached dorsolaterally through an incision in the left flank extending from the latissimus dorsalis muscle, ventral along the margin of the rib cage to the level of the sternum. Ventral retraction of the spleen and the kidney allowed for the dissection of nerves located along the splenic and renal blood vessels. In eight rats sympathetic nerve activities from the renal and splenogastric nerves were recorded simultaneously using stainless steel bipolar hook electrodes. The activities of the renal and splenogastric nerves were recorded from the proximal ends of the nerves, the cut ends of which were anchored to the distal poles of the electrodes. In a second group of eight rats nerve activities were recorded from the renal and lumbar sympathetic nerves. Limited access, deep within the posterior musculature, required that the lumbar sympathetic chain be left intact during recording. Nerve activity was amplified in two stages using Grass Instruments P15 and P511 amplifiers (bandpass 0.1–3 kHz). The nerve signals were rectified, integrated, and displayed along with arterial blood pressure on a Beckman polygraph. Data were stored on magnetic tape for subsequent analysis.

At the end of each experiment the nerves were sectioned, leaving an isolated segment on each electrode. Recordings from these segments provided estimates of the background level for nerve activity. This level was later subtracted from all activities measured in intact nerves to obtain estimates of true sympathetic activity.

### *Analysis of Nerve Signals*

Integrated nerve signals were digitized by computer. Fifty seconds of digitized data were sampled during four different experimental conditions: *1*) with spinal cord intact, *2*) 20–30 min after $C_1$ spinal transection, *3*) after ganglionic blockade hexamethonium (20 mg/kg) or chlorisondamine (2.5 mg/kg) and finally, *4*) after section of both proximal and distal portions of the nerves.

Average nerve activity and mean arterial blood pressure were calculated for each of the 50-s experimental periods. Within each group of animals, average nerve activity and blood pressure were compared between intact, spinally transected, and ganglionically blocked rats using a one-way analysis of variance (repeated measures) in which a value of $P < 0.05$ was considered significant.

The temporal relationships between simultaneously recorded nerve activities, before and after transection, were studied using cross-correlation analysis. Several 50-s periods of nerve activity were sampled under each condition, and the maximum normalized values of $\rho$ were computed for each correlogram. Correlations of multiple samples, taken under identical conditions, were compared to ensure the repeatability of our analysis and to detect false correlations resulting from temporary locking of shifting periodicities. Differences between mean $\rho$ values for intact and transected animals were compared within groups using a paired $t$ test.

Power spectral densities were also computed for the same data before and after spinal transection. The spectra were normalized and examined for periodicities occurring between 0 and 10 Hz.

## RESULTS

### *To What Extent is Supraspinal Drive Necessary for Maintenance of Sympathetic Activity?*

Immediately upon spinal transection, there was a rapid, but transient, increase in arterial blood pressure and heart rate. This rapid rise in arterial pressure was usually accompanied by a sharp increase in renal and splenogastric sympathetic activities (Fig. 1). Within several minutes after spinal transection, arterial pressure decreased to levels significantly below control, whereas heart rate remained slightly elevated (20%). During this period, renal and splenogastric sympathetic nerve activities increased to approximately twice their control levels (Figs. 1 and 2). Sympathetic activity in the lumbar chain decreased (Fig. 1*B*).

Ganglionic blockade significantly reduced sympathetic nerve activity below both intact and transected levels (Fig. 3, *A* and *B*). Mean arterial blood pressure, already reduced after spinal transection, was reduced somewhat further by ganglionic blockade (Fig. 3*C*).

### *How Does Spinal Transection Alter Synchronization of Sympathetic Discharges?*

In intact rats ($n = 8$) renal and splenogastric activities exhibited a wide range of correlations (normalized $\rho$ values ranged from 0.38 to 0.89). There was a direct relationship between the degree of correlation and the incidence of common periodicities, as determined by power spectral analysis (Fig. 4). These periodicities were sometimes at the frequency of the respirator (1.3 Hz), but they also occurred above or below that frequency. The degree of correlation was not related to the average levels of sympathetic activity, either before or after transection. There was no relationship between $\rho$ values and blood pressure before or after transection.

Spinal transection significantly reduced the average degree of correlation between renal and splenogastric

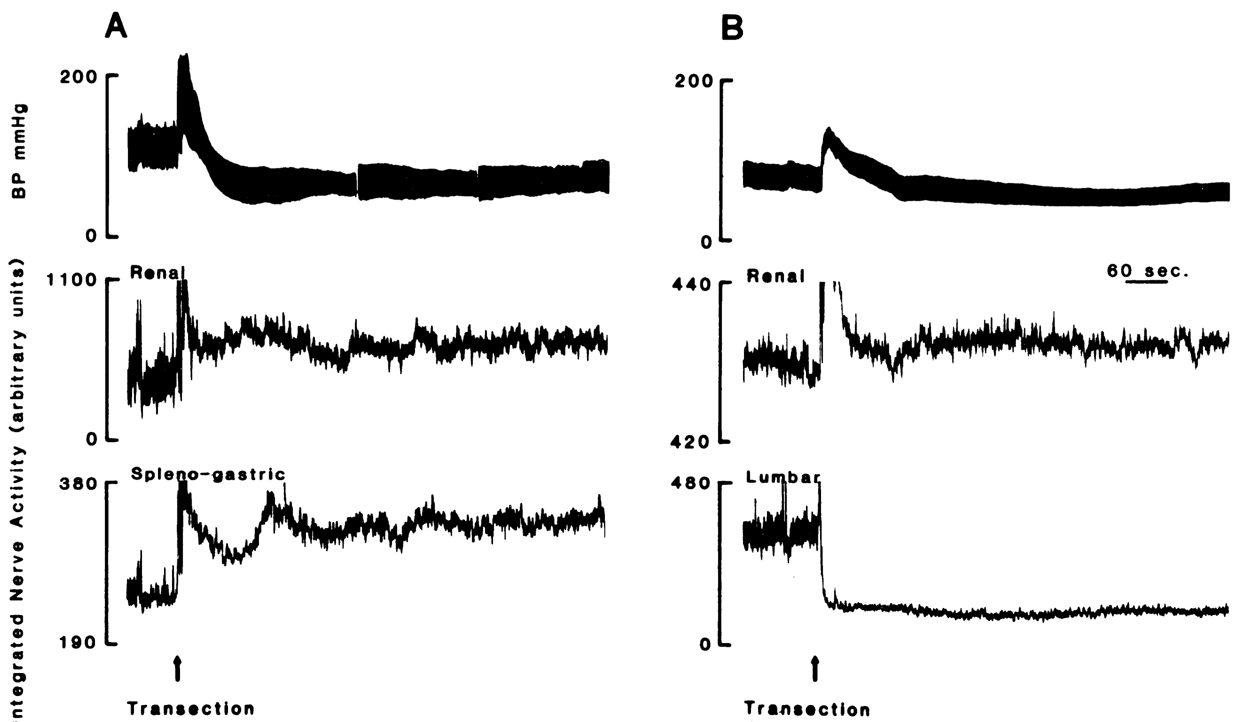


FIG. 1. Responses of integrated sympathetic nerve activity to cervical spinal cord transection. Neural signals have been corrected for background noise levels. *A*: blood pressure (*top*), renal nerve activity (*middle*), and splenogastric nerve activity (*bottom*). $C_1$ cord transection indicated at *arrow*. *B*: blood pressure (*top*), renal nerve activity (*middle*), and lumbar chain nerve activity (*bottom*). $C_1$ cord transection indicated at *arrow*.

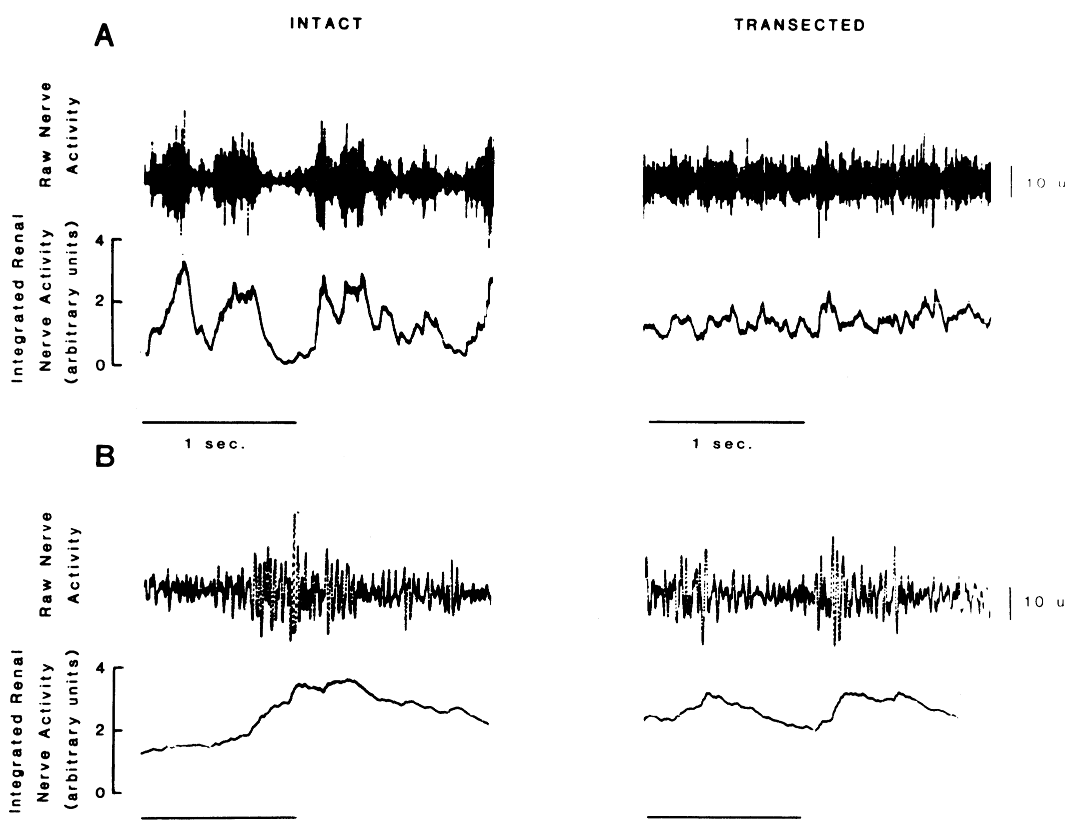


FIG. 2. Response of renal nerve activity to cervical spinal cord transection. *A*: slow time scale (1 s) of raw (*top*) and integrated (*bottom*) sympathetic nerve activity before and after cord transection. *B*: fast time scale (200 ms) of raw (*top*) and integrated (*bottom*) sympathetic nerve activity before and after cord transection.

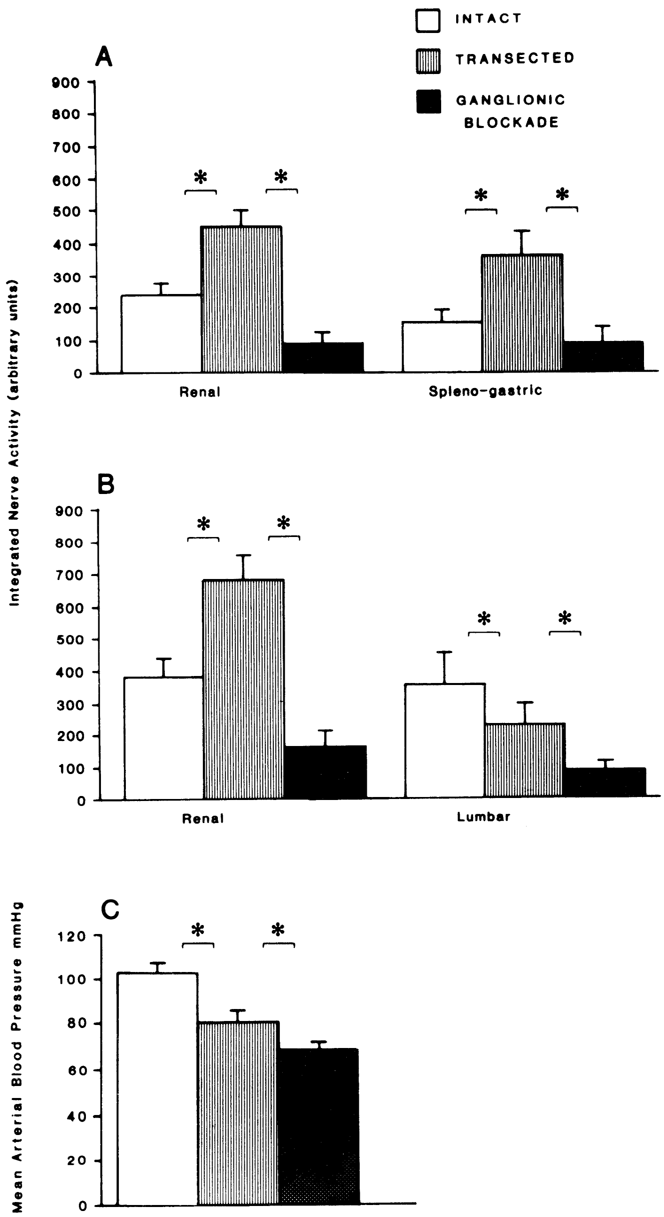


FIG. 3. Effect of cervical cord transection ($C_1$) and ganglionic blockade on integrated sympathetic nerve activity and blood pressure. Neural signals have been corrected for background noise levels. *A*: average responses (±SE) for renal and splenogastric nerve activity in 8 rats. *B*: average responses (±SE) for renal and lumbar nerve activity in 8 rats. *C*: average arterial blood pressures (±SE) for 16 rats. * $P < 0.05$.

activities (Figs. 4–6). Values of $\rho$ fell dramatically for the five rats that had exhibited high correlations in the intact state. Transection caused smaller changes in the values of $\rho$ for rats that had exhibited relatively low correlations before transection (Fig. 4). Predictably those rats that exhibited the greatest decrease in internerve synchrony were the rats that, after transection, lost major common periodicities in their activities.

In intact rats average $\rho$ values for renal and lumbar activities were slightly lower than those for renal and splenogastric activities (mean = 0.48), and they showed greater variability between rats (Fig. 6*B*). The presence of common periodicities in renal and lumbar activities was rare. Transection was accompanied by substantial reductions in the degree of correlation between only some renal and lumbar activities, and the decrease in the average value of $\rho$ in these rats was not statistically significant (Fig. 6). Again, there was no relationship between $\rho$ values and blood pressure before or after transection.

When sympathetic activities were highly periodic in intact rats, transection either eliminated the periodicities altogether or it changed the periods of the activities. Spectra that exhibited marked periodicities near the respiratory rate (1.3 Hz) exhibited a relative shift of power to lower frequencies after spinal transection. On the other hand, transection increased the relative power at higher frequencies in nerves which, when intact, had exhibited activities at very low frequencies (Figs. 4 and 7). There were no significant spectral peaks between 5 and 10 Hz in any of the sympathetic activities, before or after spinal transection.

## DISCUSSION

### *To What Extent is Supraspinal Drive Necessary for Maintenance of Sympathetic Activity?*

The decrease in lumbar sympathetic activity that we observed after spinal transection is consistent with changes previously reported in nerves that contain cutaneous and skeletal muscle vasoconstrictor axons (3, 11–13, 22). Since a number of these studies were conducted in animals with chronically transected spinal cords, it is unlikely that spinal shock could account for these reductions in activity. On the contrary, it seems safe to conclude that spinal systems do not generate substantial cutaneous or skeletal muscle vasoconstrictor sympathetic activity after cervical spinal transection in any animal studied so far. In the present study, spinal systems were able to maintain renal and splenogastric sympathetic activities after spinal transection. Indeed the increase in these activities that we observed after transection suggests that spinal sympathetic generators are tonically inhibited in intact rats.

The increases in renal and splenogastric nerve activities that we observed after spinal transection in rats do not agree with previous reports on the effects of acute spinal transection on abdominal sympathetic activity in cats. Although Meckler and Weaver (16) did not observe a decrease in splenic activity after transection, neither did they observe an increase. On the other hand, acute transection clearly reduced renal sympathetic activity in their cats. A similar decrease in greater splanchnic nerve activity was observed by Gootman and Cohen (11) >12 h after transection in cats. On the other hand, Ardell et al. (Ref. 3, Fig. 1) found that, although there was virtually no hexamethonium-blockable renal nerve activity 2 days after spinal transection in cats, there was substantial activity after 14 days. Therefore we consider the hypothesis still tenable that differences observed between cats and rats after acute spinal transection may be due to differences in either the duration of spinal shock or in the rate of development of compensatory changes in these species.

Conceivably, renal and splenogastric activities in our rats were driven by nociceptors. Afferents from the flank

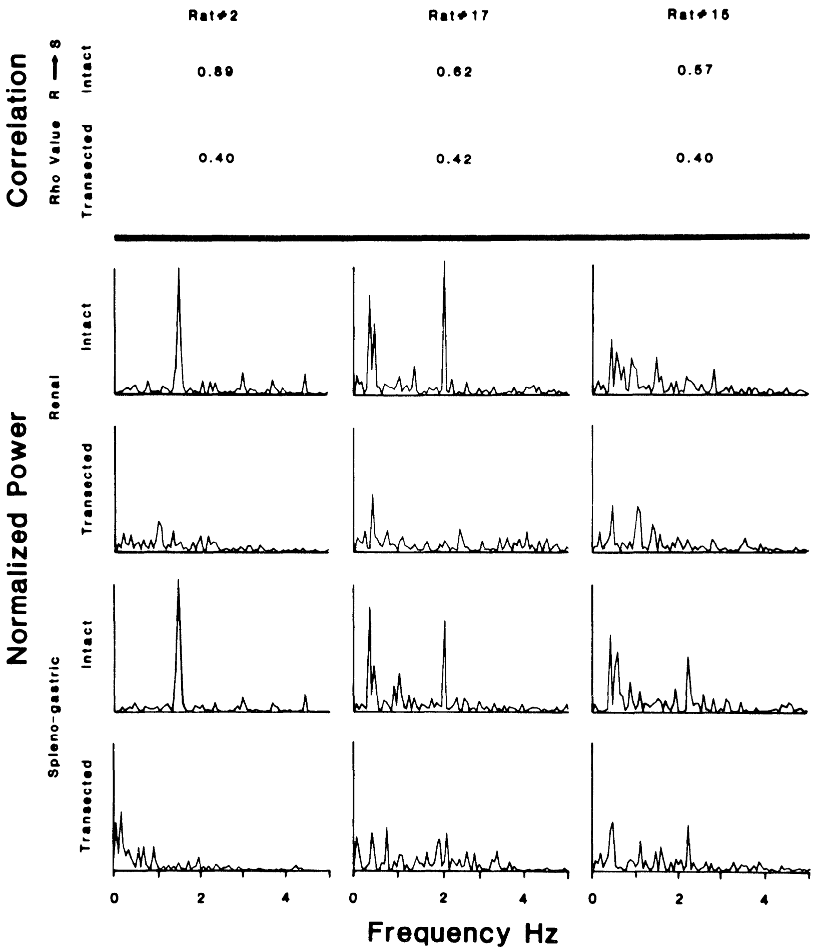


FIG. 4. Cross-correlation and power spectral analysis before and after cord transection. *Top*: normalized maximum (zero lag) ρ values for 3 rats showing representative responses to cord transection. *Bottom*: normalized power spectra for same 3 rats showing common periodicities between renal and splenogastric sympathetic nerve activities. Power scale is 0–0.25 (out of 1.00) units for *rat 2* and 0–0.165 for other rats.

incision through which we recorded nerve activities or from the kidney, which was retracted in all experiments, would be expected to have more of an influence on the spinal segments related to the renal and splenogastric outputs than on those related to lumbar output. Thus afferent activity could account for the selective increase in abdominal sympathetic activity. We know of no data from the rat that would refute this hypothesis. However, spinal afferents are not responsible for the generation of ongoing sympathetic activity in acute spinal cats (16).

In the rat, there appear to be substantial differences in the abilities of spinal systems to generate renal and splenogastric activity on the one hand and lumbar activity on the other hand. If the changes in these activities are representative of changes in activity to abdominal viscera and to the body wall, respectively, then these differences could help explain why there is a transection-induced decrease in arterial pressure in the face of elevated abdominal sympathetic activity. The vascular resistances of the tissues of the body wall are heavily

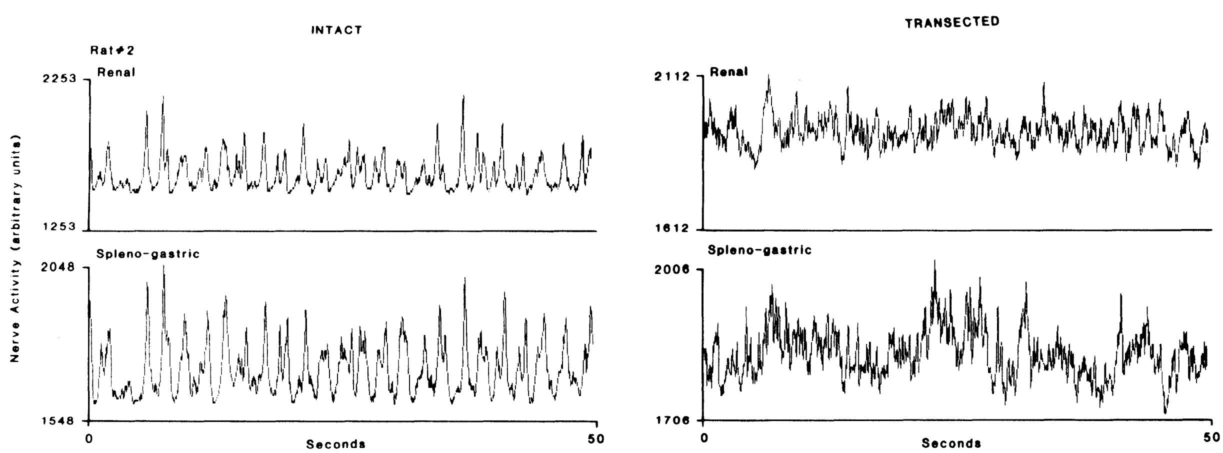


FIG. 5. Effect of transection on representative rectified and integrated nerve signal. Intact animal shows strong correlation between renal and splenogastric sympathetic nerve activities ($\rho$ = 0.89). Transection disrupts this correlation ($\rho$ = 0.40). Normalized power spectra for these records are presented in Fig. 4. *Vertical scales* are in arbitrary units.

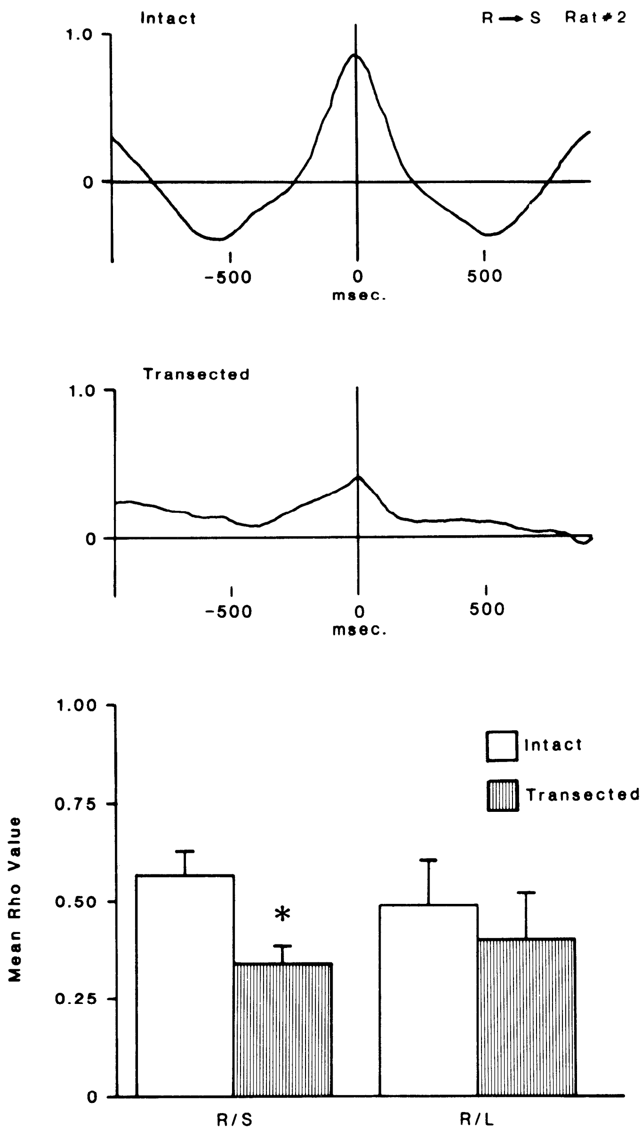


FIG. 6. Effect of cord transection on synchronization of sympathetic nerve activities. *A*: cross-correlogram of an individual animal showing marked reduction in synchronization between renal and splenogastric nerve activity. Nerve activities from which this correlogram was generated are shown in Fig. 5. Power spectra for this record are shown in Fig. 4. *B*: changes in synchronization after cord transection (mean ± SE, * $P < 0.05$) for renal and splenogastric nerves (R/S) and renal and lumbar nerves (R/L).

dependent on sympathetic activity (9). Generalized decreases in sympathetic activity to these tissues would be expected to cause substantial decreases in their resistances. On the other hand, the vascular resistances of abdominal viscera are more strongly determined by these organs' autoregulatory properties. For instance, renal autoregulation seriously compromises renal vascular responsiveness, both to catecholamines (15) and to renal nerve stimulation (6, 20). Indeed, even twofold increases in renal sympathetic activity are unable to increase renal vascular resistance at reduced arterial pressures in rats (17). Thus the net effect of a decrease in sympathetic activity to the tissues of the body wall and a concomitant increase in activity to the abdominal viscera would be a marked decrease in total peripheral resistance.

The effect of this decrease in resistance on arterial pressure was apparently uncompensated by the small increase in heart rate (20%) which occurred in the rat after spinal transection (17). Since the dose of Flaxedil used in the present study was sufficient to block the vagus (7, 13, 18), it is probable that this increase in heart rate was due exclusively to an increase in cardiac sympathetic nerve activity. Thus posttransection increases in sympathetic activity were not restricted to the innervation of the abdominal viscera.

The results of ganglionic blockade suggest that there is significant, though limited, neurogenic support of blood pressure in the spinal rat. On the other hand, since ganglia were blocked several hours after the attainment of the steady-state increase in renal nerve activity, we cannot rule out the possibility of a secondary effect of renal sympathetic activity on arterial pressure via the renin-angiotensin system.

### *How Does Spinal Transection Alter Synchronization of Sympathetic Discharges?*

Discharges in renal and splenogastric sympathetic activities were synchronized to varying degrees in different rats. The incidence of strong correlations between activities was often related to the incidence of marked periodicities at, or near, the respiratory rate. Thus it would appear that synchrony in these nerves is largely dependent on descending drive from brain stem systems with close relationships to respiratory rhythms.

The source of the respiratory rhythm that we observed in sympathetic activity is not clear. It was not caused by mechanical or electrical artifact from the diaphragm, for spinal transection, which would have had no effect on these factors, usually reduced the correlations. A respiratory rhythm could have been generated by feedback from intrathoracic receptors. This hypothesis is supported by the observation in several rats that their major sympathetic periodicity was identical in frequency to the respiratory rate. Attempts to abolish this rhythmicity by vagotomy in a small series of rats were not uniformly successful, indicating either that thoracic afferents were unimportant in generating the periodicities or that the relevant afferents in these rats were extravagal. Several rats exhibited marked periodicities at frequencies other than that of the respirator (see Fig. 4, *rat 17*). Generation of these periodicities may have been truly independent of central respiratory rhythms. On the other hand, these periodicities may have manifested central respiratory rhythms that simply were not coupled to our respirator.

Several laboratories have reported that spinal transection reduced or abolished the synchrony between activities in sympathetic nerves (3, 11). In some of those experiments, either systemic hypoxia or stimulant drugs were used to bring sympathetic activity to usable levels for correlation analysis. In our rats the average levels of renal and splenogastric activities were not only well maintained, but increased after spinal transection. Therefore reductions in synchrony in our rats could not have been secondary to a generalized reduction in the average level of activity or to a reduction in signal-to-noise ratio.

Gootman and Cohen (11) were able to measure con-

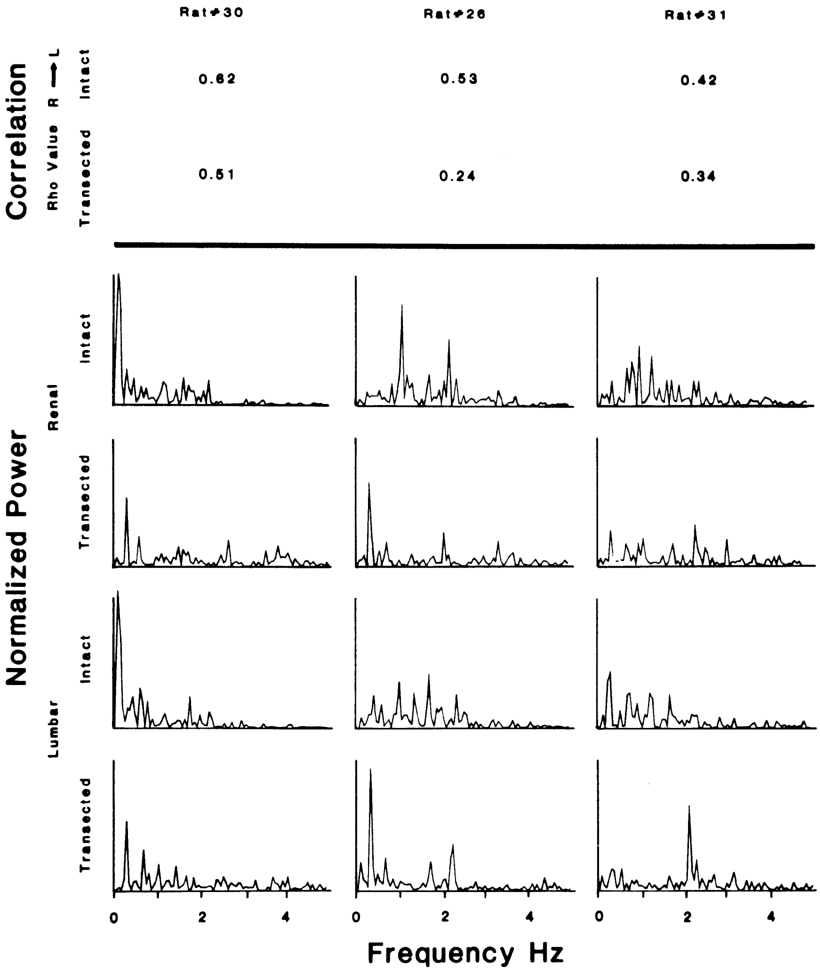


FIG. 7. Cross-correlation and power spectral analysis before and after cord transection. *Top*: $\rho$ values for 3 rats showing representative responses to cord transection. *Bottom*: normalized power spectra for 3 rats showing common periodicities between renal and lumbar chain sympathetic nerve activities. Power scale is 0–0.165 (out of 1.00) units for all rats.

sistent temporal offsets between cervical and splanchnic nerve activities using cross-correlograms. We would like to have been able to measure similar offsets between the sympathetic activities of our three nerves to determine the relative locations of the generators of their activities before and after transection. Unfortunately, distances along the rat spinal cord are small, and offsets of only a few milliseconds would be expected. Differences of this magnitude were impossible to detect.

The majority of the periodicities of sympathetic activity in previous studies, all conducted in cats, can be accounted for by oscillations at frequencies between 2 and 10 Hz (3, 11). We never observed significant periodicities at these frequencies. The absence of a clear cardiac rhythmicity in any of this series of rats was surprising, for we have seen cardiac rhythmicities in other series. In those rats, transection always abolished periodicities at the cardiac rate.

Gootman and Cohen (11) noted the evolution of very low-frequency sympathetic activity on spinal transection in the cat. We noted a similar phenomenon in a substantial number of our rats. However, transection also caused a broad increase in low-frequency power in some rats, with little indication of the emergence of new major periodicities. It seems likely that the inherent periodicities of spinal systems in the rat lie below 1 Hz and that they are easily "captured" or driven by descending systems in the intact animal.

Barman et al. (5) demonstrated brain stem neurons whose activity was specifically correlated to sympathetic activity projecting to restricted regions. They suggested that this specificity may manifest a significant degree of specificity in the brain stem generators of sympathetic activity. Although in intact rats renal and splenogastric activities often exhibited common periodicities, this was not always the case. Independence of major periodicities was most likely when neither activity exhibited a strong respiratory frequency. After spinal transection, there was a general decrease in strong periodicities in the activity of each nerve and an increase in the independence of periodicities between activities of nerves in the same rats. These changes corresponded to diminished values of $\rho$ for the cross-correlations.

Lumbar and renal nerve activities less frequently exhibited common periodicities, either before or after transection. The large variation in observed $\rho$ values complicates the interpretation of these data. Failure of spinal cord transection to significantly reduce the correlation between renal and lumbar nerve activity may support the notion that their respective spinal generators are linked. A closer examination of the sources of the variability in these rats revealed three types of responses to transection. One rat exhibited a very high correlation between renal and lumbar activities, which was not reduced by transection, suggesting (in this rat) a very strong linkage between renal and lumbar spinal sympathetic generators. Other rats exhibited moderate correlations that were substantially reduced by transection, suggesting (in these rats) a greater dependence on common supraspinal sympathetic generators. Finally, some rats exhibited low $\rho$ values that were not substantially reduced by transection, suggesting (in these rats) a marked independence of both supraspinal and spinal generators of renal and lumbar sympathetic activity.

Thus spinal transection did not significantly reduce the average $\rho$ values for correlations between renal and lumbar activities (Fig. 6), on the one hand, because one rat exhibited high correlations (and similar power spectra) before and after transection and, on the other hand, because several rats exhibited little correlation either before or after transection. Therefore the correct interpretation of Fig. 6 is that, between rats, there is a wide range of independence between both spinal and supraspinal generators of renal and lumbar sympathetic activity. The mechanisms responsible for this range of independence are the subjects of continuing research.

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