

On the Theory of Lateral Inhibition

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Zusammenfassung

Das mathematische Modell für das Prinzip der lateralen Inhibition in der Theorie der optischen Perzeption führt auf ein System nichtlinearer Gleichungen für n reelle Variable. Dieses System wird auf Lösbarkeit und eindeutige Lösbarkeit untersucht. Es zeigt sich, daß die Gleichung als Bedingung für die stationären Zustände eines geeigneten zeitabhängigen Systems zu deuten ist. Hier kann man ein diskretes und ein kontinuierliches Modell einführen. In beiden Fällen kann die Frage der Existenz der Lösungen und der Stabilität einigermaßen vollständig geklärt werden. Eine Verallgemeinerung auf kontinuierlich viele Raumvariable ist möglich.

1.

We shall investigate a special type of nonlinear systems with applications to certain theories of optical perception and pattern recognition, usually called networks with lateral inhibition. For applications and related results see the Appendix and Reichardt (1962).

The system consists of a finite number of units A_j , $j = 1, \dots, n$, each of them having a real input y_j and a nonnegative output z_j . If the units A_j are not connected then

$$z_j = b_j \vartheta(y_j - \bar{y}_j). \quad (1)$$

Here the nonlinearity ϑ is defined by

$$\vartheta(y) = \max(y, 0), \quad (2)$$

the number b_j is a positive factor and \bar{y}_j a constant threshold. If the output z_k acts inhibiting on A_j then the relation (2) has to be replaced by

$$z_j = b_j \vartheta\left(y_j - \bar{y}_j - \sum_{k=1}^n \beta_{jk} z_k\right), \quad j = 1, \dots, n, \quad (3)$$

where the nonnegative inhibition coefficient β_{jk} represents a measure for the magnitude of the inhibition between A_k and A_j . We shall exclude self-inhibition, thus

$$\beta_{jj} = 0, \quad j = 1, \dots, n. \quad (4)$$

By a simple substitution we achieve $\bar{y}_j = 0$, $b_j = 1$, i.e.

$$z_j = \vartheta\left(y_j - \sum_k \beta_{jk} z_k\right), \quad j = 1, \dots, n. \quad (5)$$

We introduce vector and matrix notation. The input of the system is $y = (y_j)$, the output $z = (z_j)$. We define a nonnegative matrix $B = (\beta_{jk})$. We shall use the following wellknown facts from matrix theory [Theorems of Perron and Frobenius, see Varga (1962)]. Let $r(B)$ be the spectral radius of B (the radius of the smallest disc with center zero containing all eigenvalues of B). Then $r(B)$ is an eigenvalue of B , and B has a nonnegative (right or left) eigenvector corresponding to $r(B)$. If all β_{jk} , $j \neq k$, are positive then $r(B) > 0$ and to $r(B)$ corresponds a uniquely determined positive eigenvector.

A reasonable question is whether in the system (5) every input y corresponds to a uniquely determined output z , i.e. whether the Eqs. (5) have a unique solution z for every fixed y .

Let y be a fixed input and z a solution of (5). Obviously each component of z satisfies $0 \leq z_j \leq \vartheta(y_j)$. Hence the solution z is contained in the convex compact (compact = closed and bounded) subset D of the n -dimensional space \mathbb{R}^n ,

$$D = \{z = (z_j) : 0 \leq z_j \leq \vartheta(y_j), \quad j = 1, \dots, n\}. \quad (6)$$

We define a continuous nonlinear mapping $T: \mathbb{R}^n \rightarrow \mathbb{R}^n$ by

$$(Tz)_j = \vartheta\left(y_j - \sum_k \beta_{jk} z_k\right), \quad j = 1, \dots, n. \quad (7)$$

The number $(Tz)_j$ is the j -th component of the image vector Tz . For each particular j we have $0 \leq (Tz)_j \leq \vartheta(y_j)$, hence T maps the whole space \mathbb{R}^n into the set D . In particular the set D is mapped into itself. We make use of a well-known result from topology (see Ljusternik and Sobolew, 1968), the

Brouwer Fixed Point Theorem. *Let T be a continuous mapping of a convex compact set $D \subset \mathbb{R}^n$ into*

itself. Then T has a fixed point in D , i.e. a point z with $Tz = z$.

For the special mapping T defined by (7) we obtain

Theorem 1. For every fixed input y the Eqs. (5) have at least one solution z .

With an additional hypothesis we can prove uniqueness. Obviously the function \mathfrak{G} has the property

$$|\mathfrak{G}(\zeta) - \mathfrak{G}(\eta)| \leq |\zeta - \eta|. \quad (8)$$

Suppose $u, v \in \mathbb{R}^n$. Then for each j

$$\begin{aligned} |(Tu)_j - (Tv)_j| &\leq \left| \mathfrak{G} \left(y_j - \sum_k \beta_{jk} u_k \right) - \mathfrak{G} \left(y_j - \sum_k \beta_{jk} v_k \right) \right| \quad (9) \\ &\leq \left| \sum_k \beta_{jk} (u_k - v_k) \right| \leq \sum_k \beta_{jk} |u_k - v_k|. \end{aligned}$$

Let assume that the β_{jk} , $j \neq k$, are positive. Then B has a unique (up to a positive factor) positive left eigenvector $(\alpha_1, \dots, \alpha_n)$,

$$\sum_j \alpha_j \beta_{jk} = r \alpha_k, \quad k = 1, \dots, n; \quad r = r(B). \quad (10)$$

From (9) we obtain

$$\begin{aligned} \sum_j \alpha_j |(Tu)_j - (Tv)_j| &\leq \sum_j \alpha_j \sum_k \beta_{jk} |u_k - v_k| \quad (11) \\ &= r \sum_k \alpha_k |u_k - v_k|. \end{aligned}$$

We define a norm $\| \cdot \|$ on the n -dimensional space by

$$\|u\| = \sum_j \alpha_j |u_j|.$$

Then the distance of two elements $u, v \in \mathbb{R}^n$ is $\|u - v\|$. From (11) follows

$$\|Tu - Tv\| \leq r \|u - v\| \quad \text{for all } u, v \in \mathbb{R}^n. \quad (12)$$

If $r < 1$ then T is a contraction with respect to the distance $\| \cdot \|$ (the application of T contracts the distance of u and v).

If some of the β_{jk} , $j \neq k$, vanish, define

$$\tilde{\beta}_{jk} = \begin{cases} \beta_{jk} & \text{if } \beta_{jk} > 0, \\ \varepsilon & \text{if } \beta_{jk} = 0, j \neq k, \\ 0 & \text{if } j = k \end{cases}$$

with $\varepsilon > 0$. Then instead of (9)

$$|(Tu)_j - (Tv)_j| \leq \sum_k \tilde{\beta}_{jk} |u_k - v_k|.$$

If $r(B) < 1$ then for ε sufficiently small the spectral radius of $\tilde{B} = (\tilde{\beta}_{jk})$ is still less than unity, and T is a contraction with respect to the corresponding norm.

A contractive mapping has at most one fixed point. Thus we proved

Theorem 2. Suppose the spectral radius $r(B)$ of B is less than unity. Then the Eq. (5) have exactly one solution.

2.

For $n = 2$ the condition of Theorem 2 is necessary for uniqueness. We put

$$B = \begin{pmatrix} 0 & \alpha \\ \beta & 0 \end{pmatrix}$$

and require $\alpha\beta \neq 1$. We discuss four cases.

Case 1. There is a solution $z_1 > 0, z_2 > 0$. Then the Eq. (5) are linear with respect to this solution,

$$y_1 = z_1 + \alpha z_2, \quad y_2 = z_2 + \beta z_1. \quad (13)$$

We express the z_j in terms of the y_k ,

$$z_1 = (y_1 - \alpha y_2) / (1 - \alpha\beta), \quad z_2 = (y_2 - \beta y_1) / (1 - \alpha\beta). \quad (14)$$

Case 2. There is a solution $z_1 > 0, z_2 = 0$. Then

$$y_1 = z_1, \quad y_2 \leq \beta z_1 = \beta y_1. \quad (15)$$

Case 3. There is a solution $z_1 = 0, z_2 > 0$. Then

$$y_2 = z_2, \quad y_1 \leq \alpha z_2 = \alpha y_2. \quad (16)$$

Case 4. $z_1 = z_2 = 0$ is a solution. Then $y_1 \leq 0, y_2 \leq 0$.

Suppose $r^2(B) = \alpha\beta < 1$. Then the four sets

$$\begin{aligned} \{y_1 > \alpha y_2, y_2 > \beta y_1\}, & \quad \{y_2 > 0, y_1 \leq \alpha y_2\}, \\ \{y_1 > 0, y_2 \leq \beta y_1\}, & \quad \{y_1 \leq 0, y_2 \leq 0\} \end{aligned} \quad (17)$$

are disjoint and cover the y_1, y_2 -plane. Thus to every y corresponds a unique z . To each positive z corresponds a unique y .

If $\alpha\beta > 1$ then the first set is the intersection of the second and the third. Therefore to every y in the

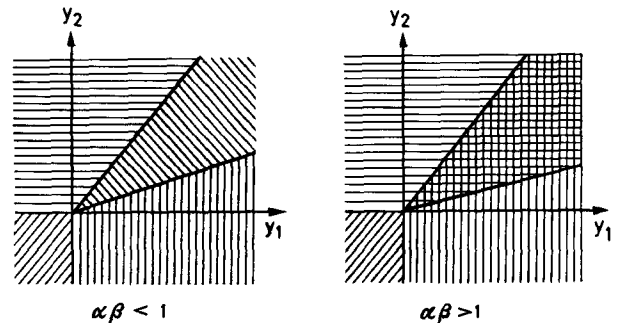


Fig. 1.

first set correspond three solutions z . Hence for $\alpha\beta > 1$ the solution is not unique in general. If $\alpha\beta = 1$ then there are some y to which correspond several positive z .

In a similar way we can discuss the set of all solutions of Eqs. (5), i.e. $Tz = z$, for $n \geq 2$.

1) If z is a positive solution then $z = y - Bz$,

$$(B + I)z = y, \quad z > 0. \tag{18}$$

2) If $z \neq 0$ is a nonpositive solution, we can assume $z_1, \dots, z_m > 0, z_{m+1} = \dots = z_n = 0$ and choose appropriate decompositions

$$z = \begin{pmatrix} \zeta \\ 0 \end{pmatrix}, \quad y = \begin{pmatrix} u \\ v \end{pmatrix}, \quad B = \begin{pmatrix} B_1 & B_3 \\ B_2 & B_4 \end{pmatrix} \tag{19}$$

of z, y, B . Then from $Tz = z$ follows

$$(B_1 + I)\zeta = u, \quad \zeta > 0, \quad B_2\zeta \geq v. \tag{20}$$

Thus the number of solutions of $Tz = z$ is either infinite or at most $2^n - 1$.

3.

As we see from the preceding paragraph, for certain choices of the inhibition matrix B and the input y there are several outputs. Since the system described in Section 1 and governed by Eq. (5) has but a single state, it is not clear on what the actual output should depend. It seems reasonable to introduce a corresponding nonstationary system with a discrete time parameter (in this context investigations of the stability of the system become meaningful, see Reichardt and MacGinitie, 1962). The nonstationary system is

$$z_j^{(v+1)} = \vartheta \left(y_j^{(v)} - \sum_k \beta_{jk} z_k^{(v)} \right), \quad v = 0, 1, 2, \dots \tag{21}$$

At the moment v the system has the state $z^{(v)}$. The input is $y^{(v)}$ and the output is $z^{(v+1)}$, the state in $v + 1$. If we write $y^{(v+1)}$ instead of $y^{(v)}$, an interpretation would be that z is determined by the input y and the inhibiting z is acting with a time lag 1.

We consider the system (21) with a stationary input

$$z_j^{(v+1)} = \vartheta \left(y_j - \sum_k \beta_{jk} z_k^{(v)} \right), \quad v = 0, 1, 2, \dots, \tag{22}$$

i.e.
$$z^{(v+1)} = Tz^{(v)}, \quad v = 0, 1, 2, \dots \tag{23}$$

A stationary solution of (23) or (22) is a solution $z^{(v)} = z$, thus $z = Tz$. Therefore the stationary solutions of (22) correspond to the solutions of Eq. (5). Hence we have the following results.

Theorem 3. *The difference Eq. (22) has a stationary solution.*

Theorem 4. *If the spectral radius of B satisfies $r(B) < 1$ then there is a unique stationary point.*

Theorem 5. *If $r(B) < 1$ then the unique stationary solution is asymptotically stable.*

Proof. If z is a stationary point and $z^{(v)}$ any other solution of (23) then

$$\|z^{(v)} - z\| \leq r \|z^{(v+1)} - z\| \leq r^v \|z^{(0)} - z\|. \tag{24}$$

Now let z be a positive stationary solution. In a neighborhood of z the system (22) is exactly linear,

$$z_j^{(v+1)} = y_j - \sum_k \beta_{jk} z_k^{(v)},$$

hence the sufficient and necessary condition for asymptotic stability is that all eigenvalues of the linear transformation lie in the interior of the unit circle, i.e. $r(B) < 1$.

This observation leads to a result of Reichardt and MacGinitie (1962): If a positive and a nonpositive stationary point exist then the positive solution is not asymptotically stable.

Let $z \neq 0$ be a nonpositive stationary point. By an appropriate reordering we can achieve $z_1, \dots, z_m > 0, z_{m+1} = \dots = z_n = 0$. Let $z + \varepsilon^{(v)}$ be a solution with $\varepsilon^{(0)}$ sufficiently small. If the obvious inequalities (20),

$$y_j = \sum \beta_{jk} z_k \leq 0, \quad j = m + 1, \dots, n$$

are strictly satisfied, then from

$$z_j + \varepsilon_j^{(v+1)} = \vartheta \left(y_j - \sum_k \beta_{jk} (z_k + \varepsilon_k^{(v)}) \right)$$

follows $z_j + \varepsilon_j^{(v)} = \varepsilon_j^{(v)} = 0$ for $j = m + 1, \dots, n$ and small $v > 1$.

Since $z_j + \varepsilon_j^{(v)} > 0$ for $j = 1, \dots, m$ and at least small v , the first m equations reduce to

$$\varepsilon_{j+1}^{(v+1)} = - \sum_{k=1} \beta_{jk} \varepsilon_k^{(v)}.$$

Therefore we have the following theorem.

Theorem 6. *A nonpositive stationary solution, defined by relation (20), is asymptotically stable if the relations*

$$r(B_1) < 1, \quad B_2\zeta > v \tag{25}$$

are satisfied.

4.

In a recent paper (Morishita and Yajima, 1972) a similar model with continuous time dependence has been investigated. A single unit of the network consists of a "lowpass filter" and the nonlinearity ϑ . The lowpass transforms the input y_j into v_j and v

transforms v_j into z_j . The outputs z_k , $k \neq j$, act inhibiting on y_j . Hence we have

$$\dot{v}_j + v_j = y_j - \sum_k \beta_{jk} z_k, \quad z_k = \vartheta(v_k). \quad (26)$$

Since ϑ is not a continuously differentiable function, it is reasonable to choose v_j as the system variable,

$$\dot{v}_j + v_j = y_j - \sum_k \beta_{jk} \vartheta(v_k), \quad j = 1, \dots, n. \quad (27)$$

Again the β_{jk} are nonnegative, $\beta_{jj} = 0$ for $j = 1, \dots, n$ and the input y_j is constant.

Theorem 7. Every solution of (27) exists for all $t \geq t_0$ and is bounded.

Proof. Suppose v is a solution for $t \in [t_0, t_1]$. Then

$$\dot{v}_j + v_j \leq y_j, \quad (v_j - y_j)' \leq -(v_j - y_j).$$

The function $u = v_j - y_j$ satisfies the differential inequality

$$\dot{u} \leq -u. \quad (28)$$

If $u(t_0) \leq 0$ then $u(t) \leq 0$ for $t \in [t_0, t_1]$. If $u(t_0) > 0$ then $u(t) \leq u(t_0) \exp(t_0 - t) \leq u(t_0)$ for $t \in [t_0, t_1]$. Therefore

$$v_j \leq y_j + \vartheta(u(t_0)) = y_j + \vartheta(v_j(t_0) - y_j), \\ \vartheta(v_j) \leq \max(v_j(t_0), y_j, 0).$$

Again from (27)

$$\dot{v}_j + v_j \geq \kappa_j, \quad \kappa_j = y_j - \sum_k \beta_{jk} \max(v_k(t_0), y_k, 0).$$

The function $\omega = \kappa_j - v_j$ satisfies (28). We conclude $\omega(t) \leq \omega(t_0) \exp(t_0 - t) \leq \omega(t_0)$, if $\omega(t_0) > 0$, thus

$$v_j \geq \kappa_j - \vartheta(\kappa_j - v_j(t_0)) \geq \min(\kappa_j, v_j(t_0)).$$

The solution remains, as far as it exists, in the compact set

$$\{v: \min(\kappa_j, v_j(t_0)) \leq v_j \leq \max(v_j(t_0), y_j, 0)\}.$$

Thus if the solution has been continued to any $t_1 \geq t_0$ then it can be continued to $t_1 + \varepsilon$, where $\varepsilon > 0$ does not depend on t_1 . Therefore the solution can be continued to every $t > t_0$. The solution is unique since the function ϑ [see (8)] and the right hand side of (27) are lipschitz-bounded.

If $v = (v_j)$ is a stationary solution of (27) then

$$v_j = y_j - \sum_k \beta_{jk} \vartheta(v_k), \quad j = 1, \dots, n. \quad (29)$$

Lemma 8. The Eqs. (5) and (29) are equivalent in the sense that there is a one-to-one correspondence between the solution sets for every fixed y and B .

Proof. We define a mapping from the solution set of (29) into the solution set of (5) by $\vartheta(v_j) = z_j$. Apply ϑ to both sides of (29), then (5) follows,

$$z_j = \vartheta(v_j) = \vartheta\left(y_j - \sum_k \beta_{jk} z_k\right).$$

Suppose u and v are two solutions of (29) which agree in all positive components. Then $\vartheta(u_j) = \vartheta(v_j)$, $j = 1, \dots, n$, and $u = v$ in view of (29). Hence if $u \neq v$ then there is at least one component where $u_j \neq v_j$ and $v_j > 0$, say. But then $\vartheta(u_j) \neq \vartheta(v_j)$ and the corresponding solutions of (5) are distinct.

On the other hand for a solution z of (5) define

$$v_j = y_j - \sum_k \beta_{jk} z_k.$$

Then

$$z_k = \vartheta\left(y_k - \sum_l \beta_{kl} z_l\right) = \vartheta(v_k)$$

and v satisfies (29). z is the image of v under the mapping $v_j \rightarrow \vartheta(v_j) = z_j$.

It follows

Theorem 9. The Eq. (29) have a solution. If $r(B) < 1$ then they have a unique solution.

In Morishita and Yajima (1972) it is asserted that the solution of Eq. (29) is unique without any further condition. This statement is obviously incorrect.

We investigate the stability of the stationary solutions.

Theorem 10. If $r(B) < 1$ then the unique solution is asymptotically stable for all y .

Proof. If v is a positive stationary solution and $v_j + \varepsilon_j$ is a neighboring solution then for t close to t_0

$$\dot{\varepsilon}_j = -\varepsilon_j - \sum_k \beta_{jk} \varepsilon_k.$$

The solution v is asymptotically stable if all eigenvalues of $(-\beta_{jk} - \delta_{jk})$ are located in the half-plane $\text{Re} \lambda < 0$, i.e. if all eigenvalues of $I + B$ are in the half-plane $\text{Re} \lambda > 0$. Sufficient for B to have this property is $r(B) < 1$.

If v is not positive, say $v_1, \dots, v_m > 0, v_{m+1}, \dots, v_n \leq 0$ then the situation becomes more complicated, the system for the ε_j is

$$\dot{\varepsilon}_j = -\varepsilon_j - \sum_{k=1}^m \beta_{jk} \varepsilon_k - \sum_{k=m+1}^n \beta_{jk} \vartheta(v_k + \varepsilon_k).$$

Define a matrix

$$I + \begin{pmatrix} B_1 & B_3 P \\ B_2 & B_4 P \end{pmatrix}$$

where $P = (p_j \delta_{jk})$ is any diagonal matrix with diagonal entries 1 or 0 and $p_j = 0$ if $v_j < 0$. The condition for asymptotic stability is now that all these matrices have their eigenvalues in the right half plane.

Again $r(B) < 1$ is sufficient. In Morishita and Yajima (1972) an example with nonconstant periodic solutions is exhibited.

5.

A natural generalization of Eq. (5) is the following. Suppose G is an open bounded domain in \mathbb{R}^d (in applications we have $d=2$) and β is a nonnegative continuous function on $\bar{G} \times \bar{G}$. Let y be a continuous function on \bar{G} . Then

$$z(s) = \vartheta y(s) - \int_G \beta(s, \sigma) z(\sigma) d\sigma \quad (30)$$

is a nonlinear integral equation similar to (5). The Eq. (30) defines a set of continuous outputs z to every continuous input y . Define a linear integral operator B by

$$(Bz)(s) = \int_G \beta(s, \sigma) z(\sigma) d\sigma \quad (31)$$

and a nonlinear integral operator T by

$$(Tz)(s) = \vartheta \left(y(s) - \int_G \beta(s, \sigma) z(\sigma) d\sigma \right). \quad (32)$$

In an appropriate space [say $L_2(\bar{G})$] T is compact and maps the set

$$D = \{z: 0 \leq z(s) \leq \vartheta y(s) \text{ for all } s \in \bar{G}\}$$

into itself. By the Schauder fixed point theorem T has a fixed point, Eq. (30) has a solution. If β is positive, then B has a positive left eigenvector. As in the proof of Theorem 1 one can show: If the spectral radius of B satisfies $r(B) < 1$ then (30) has a unique solution.

The stability theory can be extended to the equations

$$z^{(v+1)}(s) = \vartheta \left(y(s) - \int_G \beta(s, \sigma) z^{(v)}(\sigma) d\sigma \right) \quad (33)$$

and

$$\frac{\partial}{\partial t} v(t, s) + v(t, s) = y(s) - \int_G \beta(s, \sigma) \vartheta(v(t, \sigma)) d\sigma. \quad (34)$$

Walter (1971) has investigated integral equations similar to (30), where the linear operator (31) is replaced by a nonlinear integral operator.

Appendix

Nonlinear systems of the type considered in (5), (22), (27) or (29) arise in a natural way from models for the optical perception in vertebrates and insects. The so-called Hartline-Ratliff-model was investigated by Reichardt and others (see Reichardt, 1961; Reichardt and MacGinitie, 1962; Varjú, 1962; Varjú, 1965). In this model the units A_j are ommatidia of an insect eye, located on a (plane, spherical or other) surface. In the optical axis of each ommatidium A_j is a light source L_j of intensity x_j . The intensities x_k generate potentials y_j in the retinal cells of the ommatidia A_j according to

$$y_j = a_j \log \sum_k \alpha_{jk} x_k, \quad (34)$$

where the nonnegative coefficients α_{jk} may depend on the distance between L_k and A_j and on the angle between the axes of A_j and A_k .

The hypothesis of a logarithmic dependence can be supported by experimental evidence.

The ommatidium A_j generates an impulse sequence with frequency z_j . If y_j is greater than the rest potential \bar{y}_j then z_j is proportional to $y_j - \bar{y}_j$, otherwise zero. Thus the output is necessarily nonnegative.

To every input $y=(y_j)$ (potential distribution) corresponds (for sufficiently small inhibition coefficients) a frequency distribution $z=(z_j)$. The transformation $y \rightarrow z$ is of interest in at least two respects: 1) To a certain extent the transformation $y \rightarrow z$ can compensate for the loss in acuity of image in the transformation $x \rightarrow y$ (see Reichardt, 1962; Walter, 1971). 2) If only a finite set of possible intensity patterns y is given – e.g. all possible distributions of ones and zero – then in the absence of inhibition (all $\beta_{jk}=0$) the functional Σz_j will distinguish only inputs with a different number of zeros, while a system with inhibition leads to a better discrimination of patterns (Reichardt and MacGinitie, 1962). Thus the system (5) leads to a model for pattern recognition.

The aim of the present paper is to provide some mathematical theory for systems with lateral inhibition. We have shown: For arbitrary inhibition coefficients and an arbitrary input y the system has at least one possible output. In general the output is not unique. The output is unique for arbitrary inputs if the spectral radius of the inhibition matrix B is less than unity. This condition is less stringent than certain conditions in Reichardt and MacGinitie (1962) on the row sums of B . The condition is optimal, if no further information on B is provided. For arbitrary B it is a necessity to consider a nonstationary problem. The notion of stability (see Reichardt and MacGinitie, 1962) does make sense only for a nonstationary system. Stability conditions are derived. Similar results can be obtained for systems with continuous time dependence and for integral equations.

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