Periodic Solutions of Delay-Differential Equations with a Restorative Condition

Fatihcan M. Atay
Moda Cad. 214-A, Kadikoy, Istanbul 81300, Turkey
E-mail: atay@member.ams.org

Preprint 1998. Final version appeared in
Nonlinear Analysis TMA **45** (5):555–576, 2001.

Abstract

A global existence theorem is given for the periodic solutions of a class of scalar delay-differential equations satisfying a restorative condition. Properties concerning the period and the amplitude of the slowly oscillating periodic solutions are established. The results are applied to a physiological reflex model exhibiting asymmetry of response. It is shown that the model predicts periodic behavior for sufficiently large values of the delay. Furthermore, the two sources of nonlinearity in the model are shown to be responsible for different aspects of dynamics: The presence of the response asymmetry affects the local dynamics in the vicinity of an equilibrium, while the global behavior is mostly determined by the feedback in the reflex path.

Keywords: Delay-differential equation; Periodic solution; Reflex dynamics; Pupil light reflex; Response asymmetry.

1 Introduction

The scalar delay-differential equation

$$\dot{x}(t) = h(x(t), x(t-\tau)), \quad x \in \mathbf{R}, \tau > 0, \tag{1}$$

arises, among other places, in the modelling of physiological phenomena involving a time delay τ. For instance, the equation

$$\dot{x}(t) = -\alpha x(t) + f(x(t-\tau)), \tag{2}$$

where α is a positive rate constant, has been used as a model for respiration, production of blood cells, cardiac arrhythmias, and the retina of the *Limulus,* and is treated in [1] and [2]. A more general form

$$\dot{x}(t) = g(x(t)) + f(x(t-\tau)) \tag{3}$$

has been used in population models [3]. On the other hand, there are situations where a natural phenomenon can be modeled by (1) but cannot be reduced to the special cases (2) or (3). Among the examples are the reflex models exhibiting asymmetry of response, like the human pupil light reflex.

With x denoting the pupil area or the muscle activity of the iris, (2) has been used as a model for the pupil light reflex. In this case, the function f represents the feedback action in the reflex mechanism and the time delay τ is due to finite axonal conduction and neural processing times. Equation (2) is then a dynamical description of the way the pupil responds to varying levels of illumination and darkness [4]. An interesting case is the asymmetric reflex response, where α takes on different values depending on the direction of movement. For the majority of individuals, the constriction of the pupil occurs much faster than its dilation, and the observed values of α for constriction and dilation can differ by a factor of five [5]. A general approach to such problems is to allow α to be a function of the derivative $\dot{x}$, which results in an implicitly-defined differential-delay equation

$$\dot{x}(t) = -\alpha(\dot{x}(t))\, x(t) + f(x(t-\tau)), \quad x \geq 0. \tag{4}$$

Such equations have been treated in [6], and it was shown that the presence of asymmetry has important consequences for the stability of equilibria, depending on the functional form of α. Also shown was that under suitable assumptions (4) can be put into the form (1), although the resulting h in general cannot be written down explicitly in terms of its arguments. Therefore, it is desirable to consider (1) for a general function h, assuming only a few essential conditions whose validity can be assessed in the case of the reflex model (4).

The aim of this paper is twofold. First, we generalize the known facts about (2) and (3) to give a general existence result for the periodic solutions of (1) under suitable assumptions on h, and determine some properties of these periodic solutions. Second, we apply the results to models of reflex asymmetries in the form (4) to draw conclusions about oscillatory behavior in reflex systems. For the symmetric reflex model (i.e., a constant α), the existence and some properties of the periodic solutions follow from the much studied equation (2). However, the asymmetric reflex is a more realistic model in most cases, and clinical studies show the possibility of periodic oscillations [7]. Therefore, it has practical importance to determine if the asymmetric model also admits periodic solutions, and if it does, how the presence of the asymmetry affects the properties of these solutions.

Using the delay τ as a bifurcation parameter, one can obtain a local periodic solution as the equilibrium point of (1) loses its stability through a Hopf bifurcation. For more global results, fixed-point theorems on function spaces are used, in which case the assumption of the negative-feedback condition

$$xf(x) < 0 \quad \text{for } x \neq 0 \tag{5}$$

in (2) plays an essential role. The basic conclusion is the existence of a continuum of periodic solutions, bifurcating from the Hopf point and existing for each value of the delay τ for which the origin is unstable. To derive similar results for Equation (1), an analogous property needs to be determined for functions of two variables. The *restorative condition* defined in Section 2 proves to be an appropriate assumption on the function h, allowing many results of [1] and [2] to carry over to Equation (1) in a more or less straightforward way. In fact, some of the proofs apply with only minor modifications and are not repeated here. Some others, however, have subtle differences, and demand that technical details be worked out carefully. In any case, we have made an effort to keep the notation as close as possible to that of [1] and [2], in order to emphasize the parallelism of the development. After the existence and the properties of periodic solutions are established in Sections 4 and 5, we discuss the implications of the results for asymmetric reflex model (4) in Section 6.

2 The restorative condition

It will be convenient to rescale the time in (1) so that the delay is normalized to 1. This leads to an equation of the form

$$\dot{x}(t) = \lambda h(x(t), x(t-1)), \quad x \in \mathbf{R}, \lambda > 0, \tag{6}$$

where $\lambda = \tau$ appears as a parameter. In addition to (6), we will occasionally refer to the initial value problem

$$\begin{array}{lll} \dot{x}\left(t\right) = \lambda h\left(x\left(t\right), x\left(t-1\right)\right) & t \geq 1\,, & x \in \mathbf{R}\,, \quad \lambda > 0 \\ x\left(t\right) = \varphi\left(t\right) & 0 \leq t \leq 1. & \end{array} \tag{7}$$

It will be the standing assumption that for any $\varphi \in C[0,1]$ and $\lambda > 0$, there is a unique solution $x(t)$ satisfying (7). This is typically satisfied for a Lipschitz-continuous h and for φ belonging to a bounded invariant domain in the phase space $C[0,1]$, but we shall not explicitly prescribe such conditions. To emphasize the dependence of the solution $x(t)$ on φ and λ, the notation $x(t;\lambda,\varphi)$ will sometimes be used.

The function h shall be required to satisfy three sets of conditions. First, it is assumed that the origin is an equilibrium point, where h has some differentiability properties:

(H1) The function $h : \mathbf{R}^2 \to \mathbf{R}$ is continuous; $h(0,0) = 0$; h is differentiable at (0,0) and

$$C \overset{\text{def}}{=} -D_1 h(0,0) > 0, \quad D \overset{\text{def}}{=} -D_2 h(0,0) > 0,$$

with $D > C$.

Clearly, the choice of the origin does not present a loss of generality since it can be achieved by a coordinate translation. The condition $D > C$ is a necessary one for the equilibrium point to be repelling (see Proposition 1 below). One can expect sustained oscillations if there is a mechanism to push the repelled solutions back towards the origin. This is the intuitive idea behind the following *restorative condition*:

(H2) For all $x, y \in \mathbf{R}$,

- **(i)** $(h(x,y) - h(x,0))y < 0 \quad$ if $y \neq 0$, and
- **(ii)** $(h(x,y) - h(0,y))x < 0 \quad$ if $x \neq 0$.

Together with the assumption that $h(0,0) = 0$, the restorative condition implies that h is negative (resp., positive) when both its arguments are positive (resp., negative). Hence it can be thought as a generalized negative-feedback property. Notice that it also implies $h(u,u) = 0$ if and only if $u = 0$, so (6) has a unique equilibrium. Finally, the following bounds are assumed on h:

(H3) There exist positive constants Ω_1, Ω_2, and P such that

(i) $|h(x,y)| \leq \Omega_1|x| + \Omega_2|y|$ for all $x, y \in \mathbf{R}$, and

(ii) $h(0,y) \leq P$ for all $y \in \mathbf{R}$.

Note that the bound (i) in (H3) is satisfied on any compact set by the assumption in (H1) of the differentiability of h at the origin; hence, it only needs to be checked as $\|(x,y)\| \to \infty$.

In the next section the stability of the origin is investigated through the linear equation, and in Section 4 the restorative condition is summoned to prove the existence of periodic solutions.

3 The linear equation

If the function h satisfies (H1), then (6) can be linearized about the origin to obtain

$$\dot{x}(t) = -\lambda C x(t) - \lambda D x(t-1),$$

which has the characteristic equation

$$\Delta(\xi,\lambda) := \xi + \lambda C + \lambda D \exp[-\xi] = 0. \tag{8}$$

Let ω_0 be the unique solution of

$$\cos\omega_0 = -\frac{C}{D}, \quad \omega_0 \in \left(\frac{\pi}{2}, \pi\right)$$

and let

$$\omega_m = \omega_0 + 2\pi m \quad \text{and} \quad \lambda_m = \frac{\omega_0 + 2\pi m}{\sqrt{D^2 - C^2}}, \quad m \in \mathbf{Z}. \tag{9}$$

Then we have the following result.

Proposition 1 *If $\lambda > 0$ and $C \geq D > 0$, then all solutions ξ of (8) satisfy $\operatorname{Re}\xi < 0$. If $D > C > 0$, then there exists a sequence*

$$\lambda_{-2} < \lambda_{-1} < 0 < \lambda_0 < \lambda_1 < \ldots$$

given by the formulas (9), such that if $\lambda \neq 0$, then the characteristic equation (8) has a solution with real part zero iff $\lambda = \lambda_m$ for some m. If $0 < \lambda < \lambda_0$, then all solutions ξ of (8) satisfy $\operatorname{Re}\xi < 0$. If $\lambda = \lambda_m$, then (8) has a pair of complex conjugate roots $\xi = \pm i\omega_m \neq 0$; these are simple roots, and there are no other roots with zero real part. For λ near λ_m there is a unique pair $\xi_m(\lambda)$, $\overline{\xi_m(\lambda)}$ of complex conjugate roots near $\pm i\omega_m$. The function $\xi_m(\lambda)$ depends analytically on λ, satisfies $\xi_m(\lambda_m) = i\omega_m$ and its derivative satisfies

$$\operatorname{sgn}(\lambda_m) \cdot \operatorname{Re}\xi_m'(\lambda_m) > 0.$$

The proof of Proposition 1 is a direct application of Propositions A.1 and A.2 of [2] to (8).

Corollary 2 *Let $D > C > 0$ and $\lambda > \lambda_0$, where λ_0 is given by (9). Then the characteristic equation (8) has a solution ξ satisfying $\operatorname{Re}\xi > 0$ and $\operatorname{Im}\xi \in (\pi/2, \pi)$.*

Proof. Let $S = \{\xi \in \mathbf{C} : \operatorname{Re}\xi > 0 \text{ and } \operatorname{Im}\xi \in (\pi/2, \pi)\}$. By Proposition 1, if λ is greater than and close to λ_0 , then (8) has a solution in S. In fact, if $\Delta(\xi^*, \lambda^*) = 0$ for any $\lambda^* > 0$ and ξ^* satisfying $\operatorname{Re}\xi \geq 0$, then

$$\frac{\partial\Delta}{\partial\xi}(\xi^*, \lambda^*) = 1 - \lambda^* D \exp[-\xi^*] = 1 + \lambda^* C + \xi^* \neq 0;$$

hence, by the implicit function theorem there exists a continuous curve $\gamma(\lambda)$, defined on an open neighborhood of λ^*, such that $\Delta(\gamma(\lambda), \lambda) = 0$. Furthermore, noting that (8) cannot have a solution with imaginary part equal to $\pi/2$ or π, and using Proposition 1, one sees that for $\lambda > \lambda_0$, (8) does not have a solution on the boundary of S. Hence for $\lambda > \lambda_0$, $\gamma(\lambda)$ is confined to the set S. To prove the corollary, it is enough to show that γ is defined and continuous on (λ_0, ∞). Let $(\lambda_0, \bar{\lambda})$ be an interval on which γ is defined and continuous. If $\bar{\lambda}$ is finite, then for $\lambda \in (\lambda_0, \bar{\lambda})$, the solution $\xi = \gamma(\lambda)$ to (8) satisfies

$$|\xi| \leq \lambda C + \lambda D \left|\exp[-\xi]\right| \leq \bar{\lambda}(C + D);$$

therefore $\gamma((\lambda_0, \bar{\lambda}))$ lies in a compact subset of the complex plane. Then a sequence $\{\lambda_n\} \subset (\lambda_0, \bar{\lambda})$ can be found such that $\lambda_n \to \bar{\lambda}$ and $\gamma(\lambda_n) \to q$ for some complex number q. Continuity of Δ then implies that $\Delta(q, \bar{\lambda}) = 0$, which in turn implies that $q \in S$. Defining $\gamma(\bar{\lambda}) = q$ and using the fact that $\partial\Delta/\partial\xi$ is nonzero at the point $(\gamma(\bar{\lambda}), \bar{\lambda})$, it is seen that γ can be extended to an open interval containing $\bar{\lambda}$. This proves that γ is defined and continuous on (λ_0, ∞), proving the corollary. ■

Next is a lemma to be used later which compares h to its linearization on a certain subset of the plane.

Lemma 3 *Let $r > 0$, and denote $S_r := \{(x, y) \in \mathbf{R}^2 : xy \geq 0 \text{ and } ||(x, y)|| \leq r\}$ (where $\|\ \|$ is the Euclidean norm). Assume (H1) and (H2) hold. Then there exists $k > 0$ such that*

$$|h(x, y)| \geq k|Cx + Dy| \quad \textit{for all } (x, y) \in S_r, \tag{10}$$

where C and D are as in (H1). Conversely, for any $k \in (0, 1)$, there exists $r > 0$ such that (10) holds.

Proof. Fix $r > 0$. Suppose that (10) is not satisfied for any $k > 0$. Then there exists sequences $\{(x_n, y_n)\}$ in S_r and $\varepsilon_n \to 0$ as $n \to \infty$ such that

$$|h(x_n, y_n)| \leq \varepsilon_n |Cx_n + Dy_n|, \quad n = 1, 2, \ldots \tag{11}$$

Since S_r is compact, it can be assumed that $(x_n, y_n) \to (x, y) \in S_r$. Letting $n \to \infty$ gives $|h(x, y)| \leq 0$, which implies $(x, y) = (0, 0)$. By passing to a subsequence if necessary, one can assume that x_n and y_n have the same sign for all n, which we take to be positive for definiteness, so that $h(x_n, y_n)$ is negative, and (11) becomes

$$h(x_n, y_n) \geq \varepsilon_n(-Cx_n - Dy_n), \quad n = 1, 2, \ldots \tag{12}$$

Now note that the mapping $(x, y) \mapsto C|x| + D|y|$ defines a norm on $\mathbf{R}^2$. By differentiability of h at the origin

$$h(x_n, y_n) = -Cx_n - Dy_n + o\left(\|(x_n\, , \, y_n)\| \right),$$

Substituting into (12), dividing both sides by $C|x_n| + D|y_n|$ and rearranging gives

$$(1 - \varepsilon_n) \; \frac{C\, x_n + D\, y_n}{C\; |x_n| + D\; |y_n|} \;\; \leq \;\; \frac{o\,(\,\|\,(x_n, y_n)\,\|)}{C\; |x_n| + D\; |y_n|}.$$

As $n \to \infty$, the left hand side of this inequality goes to 1 while the right hand side goes to 0, leading to the contradiction $1 \leq 0$. This proves the first assertion of the lemma.

Similarly, take $k \in (0, 1)$. If (10) is not satisfied for any $r > 0$, then a sequence $\{(x_n, y_n)\}$ converging to zero can be found such that x_n and y_n have the same sign for all n and

$$|h(x_n, y_n)| < k|Cx_n + Dy_n|.$$

Again for definiteness assume that x_n, y_n are positive for all n. This implies

$$\frac{h(x_n, y_n)}{Cx_n + Dy_n} = \frac{-Cx_n - Dy_n + o\,(\|(x_n, y_n)\|)}{Cx_n + Dy_n} > k\frac{-Cx_n - Dy_n}{Cx_n + Dy_n},$$

or, after rearranging,

$$\frac{o\,(\|(x_n, y_n)\|)}{Cx_n + Dy_n} > (1 - k).$$

Letting $n \to \infty$ gives the contradiction $0 \geq 1 - k$. ■

4 Ejective fixed points and periodic solutions

We recall some definitions. If $f : X \to X$ is a continuous function on a topological space X, then a fixed point x of f is called *attractive* if there exists an open neighborhood U of x such that for every open neighborhood V of x, there exists an integer $n = n(V)$ such that $f^k(y) \in V$ for all $k \geq n$ and $y \in U$. The fixed point x is called *ejective* if there is an open neighborhood W of x such that for every $y \in W - \{x\}$ there exists an integer $n = n(y)$ such that $f^n(y) \notin W$. Finally, a subset of a Banach space is said to be infinite dimensional if it is not contained in any finite dimensional subspace.

A theorem due to F. E. Browder [8] states that if $\Psi : K \to K$ is continuous and compact, where K is a closed, bounded, convex, infinite-dimensional subset of a Banach space, then Ψ has a fixed point which is not ejective. The existence of periodic solutions of (6) will be proved by finding a suitable subset K of the Banach space $C[0, 1]$ and defining a function Ψ on this set using the solutions of (7) corresponding to initial functions taken from K. An element of K mapped by the solution operator into itself at a later time corresponds to a periodic solution, although possibly a constant one. The trivial solution is the only equilibrium for (6), and it will be shown that when it is unstable it is an ejective fixed point for the map Ψ that will be defined. Browder's theorem will then imply the existence of a nonconstant periodic solution. This approach was used in [1] to prove the existence of periodic solutions of (2).

For a fixed positive value of λ, define the sets

$$K = \{\psi \in C[0, 1] : \psi(0) = 0 \text{ and } \psi(t) \geq 0 \text{ for } t \in [0, 1]\}, \tag{13}$$

$$K_\lambda = \{\psi \in K : \exp[\lambda\Omega_1 t]\psi(t) \text{ is nondecreasing on } [0, 1]\}, \tag{14}$$

where Ω_1 is as in the hypotheses (H3). Note the following property of K_λ: For any $\psi \in K_\lambda$, $\psi(s) = 0$ implies that $\psi(t) = 0$ for all $t \in [0, s]$. It is also easy to check that K_λ is a closed, convex, infinite-dimensional subset of the Banach space $C[0,1]$ with the sup norm $\| \, \|$. The next lemma will help define a suitable compact map on a bounded subset of K_λ.

Lemma 4 *Suppose the function h satisfies the hypotheses (H1)–(H3). Let λ satisfy $\lambda > 1/D$, with D as in (H1), let φ be a nonzero element of the set K_λ defined in (14), and $x(t) = x(t; \lambda, \varphi)$ be the corresponding solution of (7). Then the following hold:*

(i) *x has denumerably many zeros $z_1 < z_2 < \dots$*

(ii) *$z_1 > 1$, and $z_{k+1} - z_k > 1$ for $k = 1, 2, 3, \dots$*

(iii) *$\dot{x}(z_{2k-1}) < 0$, $\dot{x}(z_{2k}) > 0$ for $k = 1, 2, 3, \dots$*

(iv) *The function $\exp[\lambda\Omega_1 t] \cdot x(t)$ is nonincreasing on the intervals $(z_{2k-1}, z_{2k-1} + 1)$ and nondecreasing on the intervals $(z_{2k}, z_{2k} + 1)$, $k = 1, 2, 3, \dots$*

(v) *For every $M > 0$ there exists a constant C_M such that from $||\varphi|| \le M$ follows $z_2 \le C_M$.*

(vi) *If P is as in (H3), then $||\varphi|| \le \lambda P$ implies that $x(t; \lambda, \varphi) \le \lambda P$ for $t \ge 0$.*

Remark 5 *If (H1)–(H3) hold and $\lambda \ge \lambda_0$, where λ_0 is given by (9), then*

$$\lambda > \frac{\pi}{2\sqrt{D^2 - C^2}} > \frac{1}{D}$$

hence the conditions of the lemma are fulfilled when the equilibrium point is unstable.

Proof of Lemma 4. Let $M > 0$, $\lambda > 1/D$, and φ be a nonzero element of K_λ such that $||\varphi|| \le M$. Since $\lambda D > 1$, there exists $k \in (0, 1)$ such that $k\lambda D > 1$, and by Lemma 3 there exists $r > 0$ such that $|h(x, y)| \ge k|Cx + Dy|$ whenever $(x, y) \in S_r$, where S_r is as defined in the same lemma. By choosing a smaller r if necessary, we can assume that $r \le M$. Note that $x(1) \ge 0$, and by (H2), $\dot{x}(t) \le 0$ for $t \ge 1$ as long as $x(t)$ stays positive. We will prove that $x(t)$ eventually becomes negative. Let

$$t_1 = \inf\{t \ge 2 : x(t) \le r\}.$$

If $x(2) \le r$ then $t_1 = 2$. Now assume $x(2) > r$. Define d by

$$-d = \max\{h(x, y) : r \le x, y \le M\}.$$

If $t \ge 2$, as long as $x(t) > r$ we have

$$\dot{x}(t) = \lambda h(x(t), x(t-1)) \le -\lambda d$$

so that $x(t) \le M - \lambda d(t - 2)$. Hence t_1 is finite and

$$t_1 \le 2 + \frac{M - r}{\lambda d}.$$

Define $z_1 = \inf\{t \geq 1 : x(t) \leq 0\}$. Suppose $z_1 \geq t_1 + 1$. Then $x(t) \geq 0$ if $t_1 \leq t \leq t_1 + 1$. Also for $t \in [t_1 + 1, t_1 + 2]$, we have $r \geq x(t-1) \geq x(t_1 + 1)$ since $x(t)$ is decreasing on this interval; hence as long as $x(t) \geq 0$, we have

$$\dot{x}(t) \leq -k\lambda(Cx(t) + Dx(t-1)) \leq -\ k\lambda Dx(t-1) \leq -\ k\lambda Dx(t_1+1),$$

implying

$$x(t) \leq x(t_1+1) \cdot [1\ -(t-\ t_1-1)k\lambda D]$$

for $t \in [t_1+1, t_1+2]$. Since $k\lambda D > 1$, the right-hand-side of the last inequality becomes negative for $t = t_1 + 2$. It then follows that

$$z_1 \leq t_1 + 2 \leq 4 + \frac{M\ -\ r}{\lambda d}.$$

If $z_1 \geq 2$, then $\dot{x}(z_1) = h(0, x(z_1 - 1)) < 0$ by the definition of z_1 and property (H2). To show that the same inequality also holds for $z_1 < 2$, we argue by contradiction. Suppose that $z_1 < 2$ but $\dot{x}(z_1) = 0$, i.e. $h(0, x(z_1-1)) = 0$. This implies by (H2) that $x(z_1 - 1) = \varphi(z_1 - 1) = 0$, which in turn implies that $\varphi(t) = 0$ for all $t \in [0, z_1 - 1]$, since φ belongs to K_λ. Using the hypothesis (H3) we obtain for $t \in [1, z_1]$,

$$0 \geq h(x(t), x(t-1)) = h(x(t), 0) \geq -\Omega_1|x(t)| = -\Omega_1 x(t),$$

i.e., $\dot{x}(t) \geq -\lambda\Omega_1 x(t)$. But then we have

$$x(z_1) \geq \exp[-\lambda\Omega_1(z_1 - 1)] \cdot x(1) > 0$$

which contradicts the definition of z_1. Hence $\dot{x}(z_1) < 0$.

Having shown that $x(t)$ takes on negative values in a neighborhood of z_1, it is not hard to see that $x(t)$ stays negative throughout the interval $(z_1, z_1 + 1)$. First note that the fact

$$\dot{x}(z_1) = h(0, x(z_1 - 1)) < 0$$

implies by (H2) that $x(z_1 - 1) > 0$, which, by the definition of z_1, in turn implies that $x(t-1) > 0$ for all t in $(z_1, z_1 + 1)$. Now if $x(s) = 0$ for some s in this interval, we would have

$$\dot{x}(s) = h(0, x(s-1)) < 0,$$

i.e. $x(t)$, being a C^1 function, would be strictly decreasing in a neighborhood of s. This contradiction proves that $x(t)$ is negative on $(z_1, z_1 + 1)$. Now consider the time derivative of the function $\exp[\lambda\Omega_1 t] \cdot x(t)$ for $t \in [z_1, z_1 + 1]$. Using (H2) and (H3)(i) we get

$$\begin{aligned}\frac{d}{dt}(\exp[\lambda\Omega_1 t] \cdot x(t)) &= \lambda \exp[\lambda\Omega_1 t] \cdot (\Omega_1 x(t) + h(x(t), x(t-1))) \\ &\leq \lambda \exp[\lambda\Omega_1 t] \cdot (\Omega_1 x(t) + h(x(t), 0)) \\ &\leq \lambda\Omega_1 \exp[\lambda\Omega_1 t] \cdot (x(t) + |x(t)|) = 0.\end{aligned}$$

Therefore, $\exp[\lambda\Omega_1 t] \cdot x(t)$ is nonincreasing on $[z_1, z_1 + 1]$.

Also on this interval we have

$$x(t) = \lambda \int_{z_1}^{t} h\left(x\left(s\right), x\left(s-1\right)\right) ds \geq \lambda \int_{z_1}^{t} h\left(0, x\left(s-1\right)\right) ds \geq -\lambda M_1$$

where $-M1 = \min\{h(0,y) : 0 \leq y \leq M\}$. Let $z_2 = \inf\{t > z_1 : x(t) \geq 0\}$. We know that $z_2 > z_1 + 1$ and $\dot{x}(t) \geq 0$ for $t \in [z_1+1, z_2]$.We show that z_2 is finite. Choose a positive number r_1 such that $r_1 \leq \min\{r, \lambda M_1\}$. Let

$$t_2 = \inf\{t \geq z_1 + 1 : x(t) \geq -r_1\}.$$

If $x(z_1+1) \geq -r_1$, then set $t_2 = z_1 + 1$. On the other hand, suppose $x(z_1+1) < -r_1$. If $t \geq z_1 + 1$, as long as $x(t) < -r_1$ we have $\dot{x}(t) \geq \lambda d_1$ where

$$d_1 := \min\{h(x,y) : -\lambda M_1 \leq x, y \leq -r_1\}.$$

Hence,

$$x(t) \geq -\lambda M_1 + \lambda d_1 (t - z_1 - 1)$$

implying that t_2 is finite and

$$t_2 \leq z_1 + 1 + \frac{\lambda M_1 - r_1}{\lambda d_1}.$$

Now suppose $z_2 \geq t_2 + 1$. Then $x(t) \leq 0$ for $t \in [t_2, t_2+1]$. Also, for $t \in [t_2+1, t_2+2]$ the fact that $x(t-1)$ is nondecreasing implies $x(t-1) \leq x(t_2+1)$; therefore, as long as $x(t) \leq 0$,

$$\dot{x}(t) \geq -\lambda k(Cx(t) + Dx(t-1)) \geq -\lambda k D\, x(t-1) \geq -\lambda k D\, x(t_2+1),$$

implying

$$x(t) \geq x(t_2+1) \cdot [1 - (t - t_2 - 1)k\lambda D].$$

Note that the right-hand-side of the last inequality becomes positive for $t = t_2 + 2$. Hence,

$$z_2 \leq t_2 + 2 \leq 3 + z_1 + \frac{\lambda M_1 - r_1}{\lambda d_1} \leq 7 + \frac{M - r}{\lambda d} + \frac{\lambda M_1 - r_1}{\lambda d_1}.$$

Also, since $x(t)$ is negative on (z_1, z_1+1) and $z_2 > z_1 + 1$, we have $x(z_2 - 1) < 0$, which implies that $\dot{x}(z_2) > 0$. An argument similar to the one in the previous paragraph shows that the function $\exp[\lambda \Omega_1 t] \cdot x(t)$ is nondecreasing on $[z_2, z_2+1]$. Then the function $\varphi_1(t) := x(z_2 + t)$ defined on $[0,1]$ belongs to the set K_λ, and the whole argument can be repeated to complete the proof of parts (i)- (v).

To prove (vi), let φ be an element of K_λ such that $||\varphi|| \leq \lambda P$ and let $x(t)$ be the corresponding solution of (7). On the interval $[1, z_1]$ $x(t)$ is nonincreasing and on (z_1, z_2) it is negative; therefore $x(t) \leq \lambda P$ on $[1, z_2]$. For $t \in [z_2, z_2+1]$ we have

$$\dot{x}(t) \leq \lambda h(0, x(t-1)) \leq \lambda P$$

which implies that $x(t) \leq \lambda P$ on this interval. Repeating the argument establishes (vi). ■

Let $\lambda > 0$, K_λ be given by (14), and P be as in (H3). Let $\bar{K}_\lambda$ be the set defined by

$$\bar{K}_\lambda = \{\varphi \in K_\lambda : ||\varphi|| \leq \lambda P\}.$$

Under the assumptions of Lemma 4, we can define a map Ψ_λ:$\bar{K}_\lambda \to \bar{K}_\lambda$ by:

$$\begin{array}{c} \Psi_\lambda(\varphi)(t) = x(z_2 + t; \lambda, \varphi) \\ \Psi_\lambda(0) = 0 \end{array} . \tag{15}$$

The fact that Ψ_λ maps $\bar{K}_\lambda$ into itself follows from parts (iv) and (vi) of Lemma 4. It is also not hard to show that Ψ_λ is continuous and compact. This follows from the fact that a nonzero solution $x(t; \lambda, \varphi)$ has simple zeros (part (iii) of the lemma), the numbers z_2 are uniformly bounded for all solutions (part(v) of the lemma), on bounded intervals the solution depends uniformly continuously on the initial function, and the derivatives of the solutions are uniformly bounded. We next show that for $\lambda > \lambda_0$, 0 is an ejective fixed point of Ψ_λ.

Lemma 6 . *Suppose the conditions (H1)- (H3) are satisfied and let $\lambda > \lambda_0$, where λ_0 is given by (9). Then 0 is an ejective fixed point of Ψ_λ.*

Proof. . We first claim that there exists a constant $a > 0$ such that for every $\varphi \in K_\lambda - \{0\}$ and every positive zero z of $x(t; \lambda, \varphi)$,

$$\sup_{t \geq z} |x(t; \lambda, \varphi)| \geq a. \tag{16}$$

We give the value of a as follows: Define the positive number T by

$$T = \min\left\{\frac{1}{2}, \frac{\exp[-\lambda\Omega_1]}{4\lambda(\Omega_1 + \Omega_2)}\right\},$$

where the Ω_i are as in the hypotheses (H3). By Corollary 2 the characteristic equation (8) has a solution $\xi = \mu + i\omega$ with $\mu > 0$ and $\pi/2 < \omega < \pi$; choose ε satisfying

$$0 < \varepsilon < \frac{\mu}{4} T D \sin\omega \cdot \exp[-(\mu + \lambda\Omega_1)],$$

where D is as in (H1). Define the function R by

$$R(x, y) = h(x, y) + Cx + Dy.$$

Since h is differentiable at the origin, the quotient $|R(x, y)|/||(x, y)||$ approaches zero as $||(x, y)|| \to 0$; hence, finally, choose a positive a such that

$$|R(x, y)| \leq \varepsilon ||(x, y)|| \text{ when } ||(x, y)|| \leq a,$$

where $||\cdot||$ denotes the sup norm on $\mathbf{R}^2$.

To prove (16), let φ be a nonzero element of K_λ, and denote $x(t) = x(t; \lambda, \varphi)$. Suppose that (16) is false, i.e. there exists a zero $z > 0$ such that

$$\sup_{t \geq z} |x(t)| = \delta < a.$$

Then there exists an extremum $m \in [z_n, z_n + 1]$ for some n and $|x(m)| \geq \delta/2$. For definiteness assume that m is a maximum and n is even. Now integrating by parts gives the identity

$$\int_{z_n+1+T}^{\infty} \dot{x}\,(t) \exp[-\xi t]\, dt =$$

$$-x\,(z_n + 1 + T) \exp\left[-\xi\,(z_n + 1 + T)\right] + \xi \int_{z_n+1+T}^{\infty} x(t) \exp[-\xi t]\, dt. \qquad (17)$$

Using the delay-differential equation (6), the quantity on the left-hand-side of (17) can also be written as

$$-\lambda C \int_{z_n+1+T}^{\infty} x\,(t) \exp\left[-\xi t\right]\, dt - \lambda D \int_{z_n+1+T}^{\infty} x\,(t-1) \exp\left[-\xi t\right]\, dt + \int_{z_n+1+T}^{\infty} R^*\,(t) \exp[-\xi t]\, dt$$

where we have defined $R^*(t) := \lambda R(x(t), x(t-1))$. Substituting into (17), multiplying through by $\exp[\xi(z_n + 1 + T)]$, and using the characteristic equation to substitute

$$\xi + \lambda C = -\lambda D \exp[-\xi],$$

one obtains

$$-x\,(z_n + 1 + T) + \lambda D \int_{z_n+T}^{z_n+1+T} x\,(t) \exp\left[-\xi\,(t - z_n - T)\right]\, dt =$$

$$\int_{z_n+1+T}^{\infty} R^*\,(t) \exp\left[-\xi\,(t - z_n - 1 - T)\right]\, dt \qquad (18)$$

To reach a contradiction, we first find an upper bound on the absolute value of the right-hand-side of (18)

$$\left|\int_{z_n+1+T}^{\infty} R^*\,(t) \exp\left[-\xi\,(t - z_n - 1 - T)\right]\, dt\right| \;\leq\; \varepsilon\delta \int_{z_n+1+T}^{\infty} \left|\exp\left[-\xi\,(t - z_n - 1 - T)\right]\right|\, dt$$

$$= \lambda\varepsilon\delta \int_{z_n+1+T}^{\infty} \exp\left[-\mu\,(t - z_n - 1 - T)\right]\, dt = \lambda\varepsilon\delta\mu^{-1}. \qquad (19)$$

We then find a lower bound on the absolute value of the left-hand-side of (18). Clearly, this value will be at least as big as the absolute value of its imaginary part, which is equal to

$$\begin{aligned} &\lambda D \int_{z_n+T}^{z_n+1+T} x\,(t) \exp\left[-\mu\,(t - z_n - T)\right] \cdot \sin\omega\,(t - z_n - T)\; dt \\ &\geq \lambda D \int_{z_n+1}^{z_n+1+T} x\,(t) \exp\left[-\mu\,(t - z_n - T)\right] \cdot \sin\omega\,(t - z_n - T)\; dt, \end{aligned} \qquad (20)$$

where we noted that the integrand is nonnegative since $\pi/2 < \omega < \pi$ and n is assumed to be even, and used the fact that $0 < T \leq \frac{1}{2}$. Now by Lemma (4), on the interval $[z_n, z_n + 1]$ the function $\exp[\lambda\Omega_1 t] \cdot x(t)$ is nondecreasing; therefore,

$$x(z_n + 1) \geq x(m) \exp[\lambda\Omega_1(z_n + 1 - m)] \geq \frac{1}{2}\delta \exp[-\lambda\Omega_1].$$

Using this inequality and the assumptions (H2), the magnitude of $x(t)$ can be estimated on the interval $[z_n+1, z_n+1+T]$:

$$\begin{aligned}
x(t) = x(1) + \int_{z_n+1}^{t} \dot{x}(s)\,ds &\geq x(1) - \lambda\delta(\Omega_1+\Omega_2)(t-T) \\
&\geq \delta\left(\frac{1}{2}\exp[-\lambda\Omega_1] - \ \lambda(\Omega_1+\Omega_2)(t-T)\right) \\
&\geq \delta\left(\frac{1}{2}\exp[-\lambda\Omega_1] - \ \lambda(\Omega_1+\Omega_2)T\right) \\
&\geq \frac{1}{4}\delta\exp[-\lambda\Omega_1],
\end{aligned}$$

by the definition of T. Hence, (20) is bounded from below by the quantity

$$\begin{aligned}
&\frac{1}{4}\delta\exp[-\lambda\Omega_1]\cdot\lambda D\int_{z_n+1}^{z_n+1+T}\exp\left[-\mu\left(t-z_n-T\right)\right]\cdot\sin\omega\left(t-z_n-T\right)\,dt \\
&\geq \frac{1}{4}T\delta\exp[-\lambda\Omega_1]\cdot\exp[-\mu]\cdot\sin\omega.
\end{aligned}$$

Combining with (19), we arrive at the inequality

$$\frac{1}{4}TD\exp[-(\lambda\Omega_1-\mu)]\cdot\sin\omega \leq \varepsilon\mu^{-1},$$

which contradicts our choice of ε. This completes the proof of (16).

Now choose numbers $m_n \in [z_n, z_n+1]$ such that

$$\left|x\left(m_n\right)\right| = \max_{z_n\leq t\leq z_{n+1}}\left|x\left(t\right)\right|.$$

By (H3) and Lemma 4(ii), on intervals $[z_n+1, z_{n+1}]$, $x(t)$ is nonincreasing if n is even and nondecreasing if n is odd. Hence we can actually choose $m_n \in [z_n, z_n+1]$. Equation (16) that we have just proved implies that for some positive number a,

$$|x(m_n)| \geq a/2 \tag{21}$$

for infinitely many integers n. To prove ejectivity, we need to show the existence of a positive b such that

$$x(m_{2n}) \geq b \tag{22}$$

for infinitely many integers n. We do this by using the fact that for any n, the values $x(m_n)$ and $x(m_{n+1})$ are "comparable". Indeed, choose a positive b satisfying

$$b \leq \frac{a}{2\lambda\Omega_2}$$

and suppose that $x(m_{2n}) < b$ for all large n. Then for $t \in [z_{2n+1}, z_{2n+1}+1]$ we have

$$\begin{aligned}
\dot{x}(t) = \lambda h(x(t), x(t-1)) &\geq \lambda h(0, x(t-1)) \\
&\geq -\lambda\Omega_2|x(t-1)| = -\lambda\Omega_2 x(t-1) \geq -\lambda\Omega_2 b;
\end{aligned}$$

hence,

$$x(m_{2n+1}) > -\lambda\Omega_2 b \geq -a/2$$

for all large n. But this contradicts (21). Hence (22) holds for infinitely many integers n, and the proof of the lemma is completed. ■

The previous lemma, combined with our discussion of the map $\Psi_\lambda : \bar{K}_\lambda \to \bar{K}_\lambda$ and Browder's theorem on the existence of non-ejective fixed points, immediately implies the following theorem.

Theorem 7 *Assume that the function h satisfies the hypotheses (H1)–(H3), and let λ_0 be given by (9). Then for any $\lambda > \lambda_0$, equation (6) has a nonconstant periodic solution.*

5 Slowly oscillating periodic solutions

The periodic solutions whose existence is established by Theorem 7 have the property that their successive zeros are separated by a distance greater than the delay appearing in the delay-differential equation (6), and they repeat themselves after two consecutive zeros. This follows from the fact that such solutions were obtained as the nontrivial fixed points of the map $\Psi_\lambda : \bar{K}_\lambda \to \bar{K}_\lambda$, as defined by equation (15), and from part (ii) of Lemma 4 and Remark 5. Such solutions are called *slowly oscillating*, whose definition we recall:

Definition 8 . *A periodic solution $x(t)$ of equation (6) is called a* slowly oscillating periodic solution *(SOPS) if there exist numbers $q > 1$ and $\bar{q} > q + 1$ such that*

$$\begin{aligned} &x(0) = 0, \\ &x(t) > 0 \text{ for } 0 < t < q, \\ &x(t) < 0 \text{ for } q < t < \bar{q}, \\ \text{and } &x(t + \bar{q}) = x(t) \text{ for all } t. \end{aligned}$$

Of course, the continuity of $x(t)$ implies in this definition that $x(q) = x(\bar{q}) = 0$. The relationship between SOPS and the set $\bar{K}_\lambda$, or more generally the set K_λ given by equation (14), is actually stronger than we have noted above. Indeed, let h satisfy the conditions (H1)-(H3) and $x(t)$ be a SOPS of equation (6) for some $\lambda > 0$. By uniqueness of the solutions of (7), $x(t)$ is uniquely determined by its values on the interval $[0, 1]$. For $t \in [0, 1]$, note that $x(t) \geq 0$ and $x(t - 1) = x(t - 1 + \bar{q}) \leq 0$. Using the conditions (H2),

$$\begin{aligned} \frac{d}{dt}\left(\exp[\lambda\Omega_1 t]x(t)\right) &\geq \lambda\Omega_1 \exp[\lambda\Omega_1 t]x(t) + \lambda \exp[\lambda\Omega_1 t]h(x(t), 0) \\ &\geq \lambda \exp[\lambda\Omega_1 t]\left(\Omega_1 x(t) - \Omega_1 |x(t)|\right) = 0; \end{aligned}$$

hence, if $\varphi \in C[0, 1]$ denotes the restriction of $x(t)$ to the interval $[0, 1]$, then $\varphi \in K_\lambda$.

We now present in a series of lemmas some general characteristics of slowly oscillating periodic solutions of equation (6), where the function h will be assumed to satisfy several of the hypotheses (H1)–(H3).

Lemma 9 *Let* $h : \mathbf{R}^2 \to \mathbf{R}$ *be a continuous function satisfying* $h(0,0) = 0$ *and the conditions (H2), and let* $x(t)$ *be a SOPS of equation (6) for some positive* λ*. Then* $x(t)$ *assumes its maximum on the interval* $[0,1]$ *and its minimum on the interval* $[q, q+1]$*.*

Proof. From (H2) and the definition of a SOPS it follows that $x(t)$ is nonincreasing on the interval $[1, q]$ and nondecreasing on the interval $[q+1, \bar{q}]$. ■

Lemma 10 *Let* h *be as in Lemma 9, suppose in addition that it satisfies condition (i) of (H3), and let* $\Omega_{\max} = \max\{\Omega_1, \Omega_2\}$*, where* Ω_k *are as in (H3)(i). If* $x(t)$ *is a SOPS of (6) for some* $\lambda > 0$*, then* $\lambda \geq (2\Omega_{\max})^{-1}$*.*

Proof. Let $M_+ = \max\{x(t) : t \in \mathbf{R}\}$ and $M_- = -\min\{x(t) : t \in \mathbf{R}\}$. For $t \in [q, q+1]$, we have

$$\begin{aligned} |x(t)| &\leq \lambda \int_q^t |h(x(s), x(s-1))| \, ds \leq \lambda \Omega_{\max} \int_q^t (|x(s)| + |x(s-1)|) \, ds \\ &\leq \lambda \Omega_{\max}(M_- + M_+), \end{aligned}$$

which, by Lemma 9 implies that

$$M_- \leq \lambda \Omega_{\max}(M_- + M_+). \tag{23}$$

Similarly, considering $x(t)$ for $t \in [0,1]$ and using periodicity gives

$$M_+ \leq \lambda \Omega_{\max}(M_- + M_+).$$

Adding these two inequalities gives

$$(M_- + M_+) \leq 2\lambda \Omega_{\max}(M_- + M_+).$$

Since $(M_- + M_+)$ is positive, this implies $2\lambda\Omega_{\max} \geq 1$. ■

Lemma 11 *Suppose that the function* h *satisfies the hypotheses (H1) and (H2), let* $r > 0$*, and define* $Z_r = \{(x,y) \in \mathbf{R}^2 : ||(x,y)|| \leq r \text{ and } h(x,y) = 0\}$*. Then there exists a positive constant* $\Gamma = \Gamma(r)$ *such that*

$$|x| \leq \Gamma |y| \quad \textit{for all } (x,y) \in Z_r. \tag{24}$$

Proof. By the hypotheses (H2) and the fact that $h(0,0) = 0$, it follows that if $(x, 0) \in Z_r$ then necessarily $x = 0$. Hence for $y = 0$, (24) holds for any choice of Γ. On the other hand, since Z_r is bounded, (24) can be satisfied for any fixed nonzero y if Γ is chosen large enough. Therefore, if (24) is false, there exist a sequence of points (x_n, y_n) in Z_r which are distinct from zero, and a sequence of numbers $\Gamma_n \to \infty$, such that

$$|x_n| > \Gamma_n |y_n| \text{ for all } n. \tag{25}$$

Using the compactness of the set Z_r and passing to a subsequence if necessary, we observe that $(x_n, y_n) \to (x, y)$ for some $(x, y) \in Z_r$. Letting $n \to \infty$ in (25) shows that $y = 0$, which implies as before that $x = 0$. The conditions (H2) also imply that for each n, x_n and y_n have opposite signs. Without loss of generality, we assume that x_n have the same sign for all n, and for definiteness we assume this sign to be positive, so that (25) reads

$$x_n > -\Gamma_n y_n. \tag{26}$$

We will show that (26) contradicts the hypotheses (H1). Indeed, (H1) implies that

$$h(x_n, y_n) + Cx_n + Dy_n = o(||(x_n, y_n)||).$$

Using the fact that $h(x_n, y_n) = 0$, dividing both sides by $C|x_n| + D|y_n|$, noting that the function mapping (x, y) to $C|x| + D|y|$ defines a norm on $\mathbf{R}^2$, and letting $n \to \infty$ so that $(x_n, y_n) \to (0, 0)$, we see that

$$\frac{Cx_n + Dy_n}{C|x_n| + D|y_n|} \to 0 \text{ as } n \to \infty.$$

However, using (26) and the fact that x_n are positive and y_n are negative for all n, we reach the contradiction

$$\frac{Cx_n + Dy_n}{C|x_n| + D|y_n|} > \frac{Cx_n - D\Gamma_n^{-1}x_n}{Cx_n + D\Gamma_n^{-1}x_n} = \frac{C\Gamma_n - D}{C\Gamma_n + D} \to 1 \text{ as } n \to \infty.$$

■

Lemma 12 *Suppose that the function h satisfies the hypotheses (H1), (H2), and (H3)(i), and let $r > 0$. Then there exists a constant $\bar{Q}_r > 0$ such that if $x(t)$ is a SOPS of (6) with $\max_t |x(t)| \le r$, then the minimal period $\bar{q}$ of $x(t)$ satisfies $\bar{q} \le \bar{Q}_r$. The constant $\bar{Q}_r$ depends only on r and h and not on λ .*

Proof. Let $x(t)$ satisfy the assumptions of the lemma, and let $M_+ = \max\{x(t) : t \in \mathbf{R}\}$ and $M_- = -\min\{x(t) : t \in \mathbf{R}\}$. By Lemma 3, there exists a number k_r such that

$$|\dot{x}(t)| \ge k_r |Cx(t) + Dx(t-1)|$$

when $x(t)$ and $x(t-1)$ have the same sign. For $1 \le t \le q$, $\dot{x}(t) \le 0$, as was shown in the proof of Lemma 9. Therefore on this interval

$$\frac{d}{dt}\left[\exp\left[\lambda C k_r (t-1)\right] x(t)\right] = \lambda C k_r \exp\left[\lambda C k_r (t-1)\right] x(t) + \exp\left[\lambda C k_r (t-1)\right] \dot{x}(t)$$

$$\le \lambda \exp\left[\lambda C k_r (t-1)\right] \left[C k_r x(t) - C k_r x(t) - D k_r x(t-1)\right] \le 0.$$

Hence,

$$\exp\left[\lambda C k_r (t-1)\right] x(t) \le x(1) \le M_+.$$

Thus,

$$x(t) \le \exp\left[-\lambda C k_r (t-1)\right] M_+ \le \exp\left[-\left(2\Omega_{\max}\right)^{-1} C k_r (t-1)\right] M_+ \quad \text{if } 1 \le t \le q,$$

where we have used Lemma 10 to substitute $\lambda > (2\Omega_{\max})^{-1}$. This implies that

$$0 \le x(t) \le \exp[-\delta(q-2)]M_+ \quad \text{if } q-1 \le t \le q \tag{27}$$

where $\delta = Ck_r\,(2\Omega_{\max})^{-1}$. Now let $\rho \in [q, \bar{q}]$ be a point where $x(t)$ achieves its minimum. Lemma 9 implies actually that $\rho \in [q, q+1]$. Since $h(x(\rho), x(\rho-1)) = 0$, by Lemma 11

$$|x(\rho)| \le \Gamma |x(\rho - 1)|$$

for some positive constant Γ depending on the value of r but not on λ. Combining with (27), we obtain

$$M_- = |x(\rho)| \le \Gamma \exp[-\delta(q-2)] M_+. \tag{28}$$

A similar argument results in the estimates

$$0 \ge x(t) \ge -\exp[-\delta(\bar{q} - q - 2)] M_- \quad \text{if } \bar{q} - 1 \le t \le \bar{q}$$

and

$$M_+ \le \Gamma \exp[-\delta(\bar{q} - q - 2)] M_-.$$

Combining the last inequality with (28) gives

$$M_+ \le \Gamma^2 \exp[-\delta(\bar{q} - 4)] M_+.$$

Since $M_+ > 0$, we must have $\Gamma^2 \exp[-\delta(\bar{q} - 4)] \ge 1$, which implies

$$\bar{q} \le \bar{Q}_r = 4 + \frac{4\Omega_{\max} \cdot \log \Gamma}{Ck_r}.$$

■

Lemma 13 *Suppose that the function h satisfies the hypotheses (H1), (H2), and (H3)(i). Let $J \subseteq (0, \infty)$ be any compact set such that $\lambda_0 \notin J$, where λ_0 is defined in (9). Then there exists $\kappa = \kappa(J) > 0$ such that if $x(t)$ is a SOPS of (6) for some $\lambda \in J$, then* $\max_t |x(t)| > \kappa$.

This lemma is proved in the same way as Lemma 1.6 in [2].

6 Periodic behavior in asymmetric reflex dynamics

We now consider the asymmetric reflex model (4). Rescaling the time as before, one obtains

$$\dot{x}(t) = \lambda \left[-\alpha\left(\dot{x}(t)/\lambda\right)\ x(t) + f(x(t-1))\right], \quad x \ge 0,\ \lambda > 0. \tag{29}$$

The functions α and f are assumed to satisfy the following conditions:

- **(A)** The function $\alpha : \mathbf{R} \to \mathbf{R}$ is continuous and nondecreasing, $\alpha(0) = 1$, and the derivative $\alpha'(0)$ exists. Furthermore, there exist constants α_d and α_c such that

$$0 < \alpha_d \le \alpha(u) \le \alpha_c \quad \text{for all } u \in \mathbf{R}.$$

- **(F)** The function $f : \mathbf{R}_+ \to \mathbf{R}_+$ is continuous and nonincreasing. At its unique fixed point x^*, f is differentiable and $f'(x^*) < -1$.

(We will use the notation $\mathbf{R}_+$ to mean $[0,\infty)$, and $\mathbf{R}_+^2$ to mean $\mathbf{R}_+ \times \mathbf{R}_+$.) Note that the fixed point x^* of f is an equilibrium solution of (29), and x^* is positive unless $f \equiv 0$. Also, the monotonicity of f together with $f'(x^*) < -1$ implies a negative-feedback condition with respect to the point x^*:

$$(f(x) - x^*)(x - x^*) < 0 \quad \text{for all } x^* \in \mathbf{R}_+,\ x \neq x^*. \tag{30}$$

The results of this section continue to hold if the assumption of monotonicity is replaced with the more general condition (30); nevertheless, work with a monotone f for reasons of simplicity and physical motivation. Finally note that the statement $\alpha(0) = 1$ in (A) is nothing more than a normalization convention; it can be achieved by suitably rescaling α, f, and the time.

As an implicit differential equation, it is not obvious if solutions to (29) exist at all, or if initial-value problems have unique solutions. It is reassuring that such questions turn out to have a positive answer.

Lemma 14 *Suppose (A) and (F) hold and* $\lambda > 0$.

(i) Let $\varphi : [0,1] \to \mathbf{R}_+$ *be continuous. Then there is a unique solution* $x(t)$ *satisfying (29) for* $t \geq 1$ *such that* $x|_{[0,1]} \equiv \varphi$. *Furthermore,* $x(t)$ *is bounded, nonnegative, and continuously differentiable for all* $t > 1$.

(ii) Let $I \subset \mathbf{R}_+$ *be a compact interval such that* $f(I) \subset I$, $\varphi : [0,1] \to I$ *a continuous function, and* x *the unique solution of (29) satisfying* $x|_{[0,1]} \equiv \varphi$. *Then* $x(t)$ *belongs to* I *for all* $t > 1$. *If in addition* $\varphi(1) \in \operatorname{int}(I)$, *where "int" denotes interior, then the corresponding solution* $x(t)$ *belongs to* $\operatorname{int}(I)$ *for all* $t \geq 1$.

Remark 15 *The conditions (F) guarantee the existence of an interval* I *having the property* $f(I) \subset I$, *as in statement (ii) of Lemma 14. In fact, any interval of the form* $[0, c]$, *where* $c \geq f(0)$, *has this property by the monotonicity of* f.

The proof of Lemma 14 was given in [6] and is based on the observation that, under the assumptions (A) and (F), the implicit equation (29) can be written in the form

$$\dot{x}(t) = \lambda h(x(t), x(t-1)), \quad x \geq 0,\ \lambda > 0, \tag{31}$$

for some unique and continuous function h. Indeed, for given nonnegative x and y, $h = h(x,y)$ is the unique solution of the equation

$$h = -\alpha(h)\, x + f(y). \tag{32}$$

It is in general not possible to write down an explicit description for h, but it can be compared to the simpler function

$$h_0(x,y) = -x + f(y), \tag{33}$$

which would be obtained in the case of constant α, i.e., the absence of asymmetry.

Lemma 16 *Assume that the conditions (A) and (F) hold and let* h *and* h_0 *be defined by (32) and (33), respectively. Then the following hold.*

(i) The functions $h(x,y)$ *and* $h_0(x,y)$ *have the same sign everywhere on* $\mathbf{R}_+^2$.

(ii) $|h(x,y)| \leq |h_0(x,y)|$ *for all* $x, y \in \mathbf{R}_+$.

(iii) For each compact interval $I \subset \mathbf{R}_+$, *there exists a constant* $Q \in (0,1]$ *such that*

$$|h(x,y)| \geq Q|h_0(x,y)| \quad \forall x, y \in I.$$

Proof. By the uniqueness of h and the assumption that $\alpha(0) = 1$, it is easy to see that $h(x, y) = 0$ if and only if $h_0(x, y) = 0$. Now suppose $h_0(x, y) > 0$ but $h(x, y) < 0$ for some $x, y \in \mathbf{R}_+$. Then $f(y) > x$ and $\alpha(h(x, y)) \leq 1$ since α is nondecreasing. But this leads to the contradiction

$$h(x, y) = -\alpha(h(x, y))x + f(y) > -x + x = 0.$$

Therefore $h(x, y) > 0$. Conversely, if $h(x, y) > 0$, we have $\alpha(h(x, y)) \geq 1$ so that

$$h_0(x, y) = -x + f(y) \geq \alpha(h(x, y))x + f(y) = h(x, y) > 0,$$

which proves (i). The last statement also shows that $h_0(x, y) \geq h(x, y)$ whenever it is (and hence both are) positive. Similarly, we have $h_0(x, y) \leq h(x, y)$ whenever they are negative. This proves (ii). To show (iii), fix $x \in \mathbf{R}_+$ and consider the function $g : \mathbf{R} \to \mathbf{R}$ defined by

$$g(h) = h + x\alpha(h).$$

Observe that g is strictly increasing, $g(0) = x$, g is differentiable at $h = 0$ with $g'(0) = 1 + x\alpha'(0)$, and as $|h| \to \infty$ its graph approaches a straight line with unit slope. Therefore there exists a positive constant Q^{-1} such that

$$|g(h) - x| \leq Q^{-1}|h| \quad \text{for all } h \in \mathbf{R}. \tag{34}$$

The value of Q^{-1} increases with increasing x, since $g'(0)$ does, but in a compact interval I, it may be chosen to satisfy equation (34) for all x in I. Now suppose $f(y) > x$. Then part (i) of the lemma implies that the solution h of the equation

$$h + x\alpha(h) = f(y) \tag{35}$$

is positive. Since the left side of this equality is $g(h)$, we also have $g(h) > x$; so (34) can be written as

$$g(h) - x \leq Q^{-1}h,$$

implying

$$Q^{-1}h + x \geq g(h) = h + x\alpha(h) = f(y).$$

Hence,

$$h \geq Q(-x + f(y)) = Qh_0(x, y)$$

whenever h is a positive solution of (35). Similarly, a negative solution h of equation (35) gives $h \leq Qh_0(x, y)$. Therefore,

$$|h(x, y)| \geq Q\,|h_0(x, y)|$$

for all x, y in a compact subinterval I of $\mathbf{R}_+$. That $Q \leq 1$ follows from part (ii). ■

To allow the application of the results of the previous sections to (31), the following properties of h are essential (cf. conditions (H1)-(H3) in Section 2).

Lemma 17 *(i) The function* $h : \mathbf{R}_+^2 \to \mathbf{R}$ *is continuous;* $h(x^*, x^*) = 0$*; the partial derivatives of* h *exist at* (x^*, x^*) *and satisfy* $D_2h(x^*, x^*) < D_1h(x^*, x^*) < 0$.

(ii) For any $y \in \mathbf{R}_+$*, the function* $h(\cdot, y) : \mathbf{R}_+ \to \mathbf{R}$ *is strictly decreasing. Furthermore, for all* $(x, y) \in \mathbf{R}_+^2$,

$$(h(x, y) - h(x, x^*)) \cdot (y - x^*) < 0 \quad \textit{if } y \neq x^*, \tag{36}$$

(iii) There exist positive constants Ω *and* P *such that for all* $x, y \in [-x^*, \infty)$

$$|h(x^* + x, x^* + y)| \leq |x| + \Omega|y|, \tag{37}$$

and

$$|h(x^*, x^* + y)| \leq P \tag{38}$$

Proof. The continuity of h was proved in [6]. The fact that $h(x^*, x^*) = 0$ follows from (32) by the assumptions (A) and (F). Implicit differentiation of (32) gives

$$D_1h(x^*, x^*) = -(1 + x^*\alpha'(0))^{-1}, \quad D_2h(x^*, x^*) = f'(x^*)\,(1 + x^*\alpha'(0))^{-1}; \tag{39}$$

thus $0 > D_1h(x^*, x^*) > D_2h(x^*, x^*)$, which completes the proof of (i).

Part (ii) is proved by contradiction: To prove the first statement, let $x_1 < x_2$ and assume $h(x_1, y) \geq h(x_2, y)$. By the monotonicity of α, one has $\alpha(h(x_1, y)) \geq \alpha(h(x_2, y))$, and using (32),

$$\begin{aligned} 0 &\leq h(x_1, y) - h(x_2, y) = -x_1\alpha(h(x_1, y)) + x_2\alpha(h(x_2, y)) \\ &\leq (x_2 - x_1)\alpha(h(x_2, y)) > 0. \end{aligned}$$

This contradiction shows $h(x_1, y) < h(x_2, y)$. Similarly, suppose (36) is false for some $x, y \in \mathbf{R}_+$. For definiteness, assume $y > x^*$ and $h(x, y) \geq h(x, x^*)$. Arguing as before,

$$\begin{aligned} 0 &\leq h(x, y) - h(x, x^*) = x[\alpha(h(x, x^*)) - \alpha(h(x, y))] + f(y) - f(x^*) \\ &\leq f(y) - f(x^*) = f(y) - x^* < 0. \end{aligned}$$

This contradiction shows that $h(x, y) < h(x, x^*)$. The case when $y < x^*$ is proved similarly.

To prove (37), note that the boundedness, and differentiability at x^*, of f implies the existence of a Ω such that

$$|f(x^* + y) - x^*| \leq \Omega|y|$$

whenever $(x^* + y) \in \mathbf{R}_+$. Using this inequality and statement (ii) of Lemma 16,

$$|h(x^* + x, x^* + y)| \leq |-(x^* + x) + f(x^* + y)| \leq |-x| + |f(x^* + y) - x^*| \leq |x| + \Omega|y|.$$

Similarly,

$$|h(x^*, x^* + y)| \leq |-x^* + f(x^* + y)| \leq x^* + \sup_{x \geq 0}|f(x)| := P,$$

since f is bounded. This establishes (38) and completes the proof of the lemma. ■

The function h is defined only on $\mathbf{R}_{+}^{2}$, but it can be continuously extended to the whole plane. Although such an extension will not be unique, statement (i) of Lemma 14 implies that, as far as the dynamics of equation (29) are concerned, it is immaterial how h is defined outside of $\mathbf{R}_{+}^{2}$. One particularly simple way to extend h could be to define

$$\bar{h}(x, y) = h(\max\{0, x^* + x\}, \max\{0, x^* + y\}).$$

Using Lemma 17 it is easily seen that $\bar{h}$ satisfies conditions (H1)-(H3) of Section 2. In terms of $\bar{x} = x - x^*$ one can then write (29) or the equivalent equation (31) as $\dot{\bar{x}} = \lambda \bar{h}(\bar{x}(t), \bar{x}(t-1))$,for which Theorem 7 is applicable. We will state this result in a slightly more detailed form, taking advantage of the additional properties of (29) as given in Lemma 14.

To this end, we introduce some notation. We use x^* to denote the fixed point of f as well as the constant function mapping $[0,1]$ to x^*, depending on the context. Let

$$K^* = \{\psi + x^* : \psi \in K\}, \quad K_\lambda^* = \{\psi + x^* : \psi \in K_\lambda\},$$

where K and K_λ are defined in (13) and (14). Now suppose λ is a positive number, φ is an element of K_λ^* different from x^*, and $x(t; \lambda, \varphi)$ is the solution of (29) satisfying $x|_{[0,1]} = \varphi$. Let $\bar{q}(\lambda, \varphi)$ be the second zero of $x(t; \lambda, \varphi) - x^*$ in the interval $(1, \infty)$, if such exists. This definition is unambiguous since the argument used to prove part (iii) of Lemma 4 shows that $x(t; \lambda, \varphi) - x^*$ can only have simple zeros. For each $\lambda > 0$, we will define a map $\Psi_\lambda^* : K_\lambda^* \to K_\lambda^*$ in much the same way as given by (15), but we will allow for the case that $\bar{q}(\lambda, \varphi)$ does not exist. Hence if $\bar{q}(\lambda, \varphi)$ is defined, let

$$\left(\Psi_\lambda^* \varphi\right)(t) \; = \; x\left(t + \bar{q}\left(\lambda, \varphi\right), \lambda, \varphi\right) \quad \text{for } 0 \le t \le 1.$$

If $\bar{q}(\lambda, \varphi)$ is undefined, then set $\left(\Psi_\lambda^* \varphi\right)(t) = x^*$ for $0 \le t \le 1$. Finally let

$$\Sigma \; = \; \left\{(\lambda, \varphi) \in (0, \infty) \times K^* : \varphi \in K_\lambda^* - \{x^*\} \text{ and } \Psi_\lambda^*(\varphi) = \varphi\right\}. \tag{40}$$

We then have the following result.

Theorem 18 *Suppose the conditions (A) and (F) hold, and let $I = [A, B]$ be an interval such that $f(I) \subset I$ and $A < x^* < B$. Let the set Σ be defined by (40) and let λ_0 be given by (9). Then the following hold.*

(i) There exists $\delta > 0$ such that if $(\lambda, \varphi) \in \Sigma$, then $\lambda \ge \delta$ and $\|\varphi\| < B$.

(ii) The closure of Σ in $(0, \infty) \times K^*$ is $\bar{\Sigma} = \Sigma \cup \{\lambda_0, x^*\}$.

(iii) Let $\Sigma_0 \subset \bar{\Sigma}$ be the maximal connected component of $\bar{\Sigma}$ containing (λ_0, x^*). Then Σ_0 is an unbounded subset of $(0, \infty) \times K^*$.

(iv) For each $\lambda > \lambda_0$ there exists a periodic solution $x(t)$ of (29) such that $(\lambda, \varphi) \in \Sigma_0$, where $\varphi = x\,\big|_{[0,1]}$, and $A < x(t) < B$ for all t. Furthermore, $x(t)$ is slowly oscillating in the sense that $x(t) - x^*$ satisfies Definition 8.

This result was proved in [2] for the scalar delay equation

$$\dot{x}\left(t\right) = \lambda\left[-x\left(t\right) + f\left(x\left(t-1\right)\right)\right]$$

under suitable assumptions on the function f including the negative-feedback condition (5). Since we already have available Lemmas 6, 10, 12, and 13, the same proof given in [2] works also in our case, and will not be repeated here.

It has thus been established that the model (29) for reflex dynamics admits periodic solutions. It is seen that the bounds on the amplitude of oscillations given in statements (i) and (iv) of Theorem 18 depend only on the properties of f and not on α, as long as α satisfies the conditions (A). Hence the presence of the asymmetry (i.e., if α is constant or not, or its precise shape) has no effect these bounds. The parameter that is critically dependent on α is the bifurcation value λ_0 given by (9). Comparison with (39) shows that λ_0 increases with increasing values of $\alpha'(0)$; thus increasing the steepness of α at the origin tends to stabilize the equilibrium solution. Note that this does not preclude the existence of periodic solutions since a SOPS may exist for values of λ which are less than λ_0 (see Figure 1). In fact, as Lemma 10 and equation (37) show, the lower bound on λ for the existence of a SOPS, given in part (i) of the theorem, depends only on f.

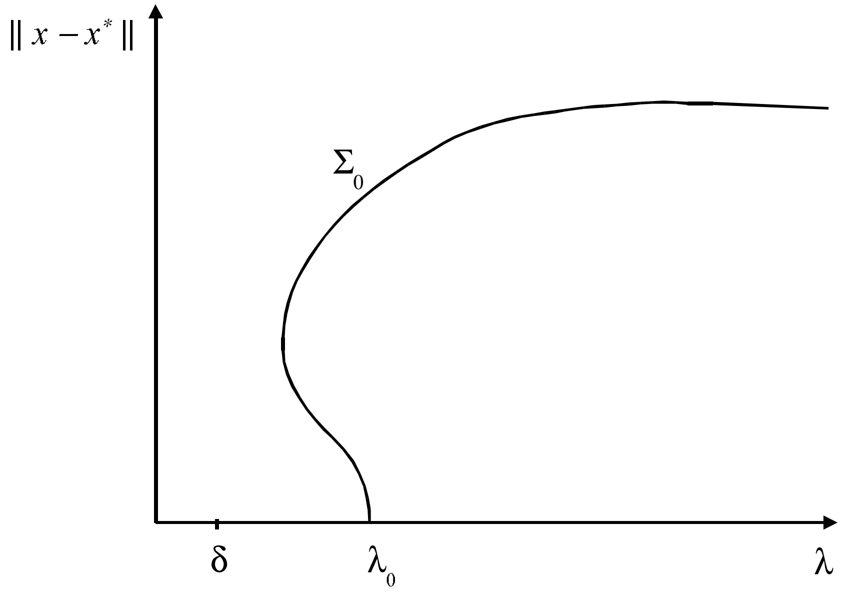

Figure 1: A global continuum of periodic solutions bifurcating from the equilibrium solution.

The properties of the periodic solutions of (29) are thus seen to depend mostly on the feedback function f. Since the stability of the equilibrium is greatly affected by the asymmetry of the reflex, it is conjectured that the two effects can be experimentally isolated. Hence, the asymmetry is perhaps best investigated through the equilibrium solution, while the study of periodic behavior could be more valuable for analyzing the feedback action in the reflex.

7 Conclusion

The global existence as well as some properties of slowly oscillating periodic solutions of a general scalar differential equation with a single delay is established under the assumption of a restorative condition. It is anticipated that the results are applicable to a large class of first-order biological or population models involving delays, since a form of restorative condition is inherent in many such systems. As a particular application, the existence of periodic solutions is proved in a model for asymmetric reflex dynamics. It is seen that the presence of asymmetry tends to stabilize the equilibrium solution, while not affecting the various bounds on the periodic solutions. It appears that the asymmetry affects local behavior, while the restorative condition, which manifests itself mainly at the feedback function, affects the global. This suggests that it may be possible to isolate the two mechanisms in experimental settings so that they are studied separately.

References

[1] HADELER K.P. & TOMIUK J., Periodic solutions of difference-differential equations, *Arch. Rat. Mech. Anal.*, **65**, 87–95 (1977).

[2] MALLET-PARET J. & NUSSBAUM R.D., Global continuation and asymptotic behaviour for periodic solutions of a differential-delay equation, *Annali di Mat. Pura ed Appl.* **145**, 33–128 (1986).

[3] KUANG Y., *Delay differential equations: with applications in population dynamics*, Academic Press, Boston (1993).

[4] LONGTIN A. & MILTON J.G., Modelling autonomous oscillations in the human pupil light reflex using non-linear delay-differential equations, *Bulletin of Mathematical Biology* **51**, 605–624 (1989).

[5] MILTON J.G. & LONGTIN A., Evaluation of pupil constriction and dilation from cycling measurements, *Vision Res.* **30**, 515–525 (1990).

[6] ATAY F.M. & MALLET-PARET J., Modeling reflex asymmetries with implicit delay differential equations, *Bulletin of Mathematical Biology* **60**, 999–1015 (1998).

[7] LONGTIN A. & MILTON J.G., Complex oscillations in the human pupil light reflex with "mixed" and delayed feedback, *Mathematical Biosciences* **90**,183–199 (1988).

[8] BROWDER F.E., A further generalization of the Schauder fixed point theorem, *Duke Math. J.* **32**, 575–578 (1965).