Feedback control in neural systems is ubiquitous. Here we study the mathematics of nonlinear feedback control. We compare models in which the input is multiplied by a dynamic gain (multiplicative control) with models in which the input is divided by a dynamic attenuation (divisive control). The gain signal (resp. the attenuation signal) is obtained through a concatenation of an instantaneous nonlinearity and a linear low-pass filter operating on the output of the feedback loop. For input steps, the dynamics of gain and attenuation can be very different, depending on the mathematical form of the nonlinearity and the ordering of the nonlinearity and the filtering in the feedback loop. Further, the dynamics of feedback control can be strongly asymmetrical for increment versus decrement steps of the input. Nevertheless, for each of the models studied, the nonlinearity in the feedback loop can be chosen such that immediately after an input step, the dynamics of feedback control is symmetric with respect to increments versus decrements. Finally, we study the dynamics of the output of the control loops and find conditions under which overshoots and undershoots of the output relative to the steady-state output occur when the models are stimulated with low-pass filtered steps. For small steps at the input, overshoots and undershoots of the output do not occur when the filtering in the control path is faster than the low-pass filtering at the input. For large steps at the input, however, results depend on the model, and for some of the models, multiple overshoots and undershoots can occur even with a fast control path.

1 Introduction

In natural environments, sensory inputs typically have a large dynamic range. For instance, the luminance input to the visual system varies over multiple log units not only between day and night, but also on much shorter
timescales (van Hateren, 1997). Likewise, the range of auditory intensities is very large, with changes in intensity often occurring on short timescales (Escabí, Miller, Read, & Schreiner, 2003). This strong dynamic nature of the input poses a problem to sensory systems because both the sensory transducers and the subsequent neurons have a limited dynamic range. Hence, to fit the input into these processing units, some form of dynamic compression is required. In this letter, we study systems in which a compression of the dynamic range is attained through an operation of gain control. Thus, the models for gain control we study operate such that, at least in their steady state, they yield a reduction in the range of their output relative to their input range.

We study two types of gain control. The first type is multiplicative gain control in which an input \( I(t) \) is multiplied by a dynamic gain \( g(t) \), which yields an output

\[
O(t) = g(t)I(t). \tag{1.1}
\]

When the gain \( g \) decreases for increasing values of the input \( I \), the dynamic range of the output \( O \) is compressed relative to the dynamic range of the input \( I \). The second type of control that we study is divisive gain control, in which an input \( I(t) \) is divided by an attenuation signal \( a(t) \), which yields an output,

\[
O(t) = \frac{I(t)}{a(t)}. \tag{1.2}
\]

When the attenuation \( a \) increases with increasing values of the input \( I \), the dynamic range of \( O \) is compressed relative to the dynamic range of \( I \). Obviously, multiplicative and divisive gain control are closely related. When the attenuation signal \( a(t) \) and the gain signal \( g(t) \) are related as \( a(t) = 1/g(t) \), the outputs \( O(t) \) of equations 1.1 and 1.2 are identical. However, as we show in section 2, for many control systems, even when \( a = 1/g \) in steady state, the dynamic behavior of \( a(t) \) and \( g(t) \) is not related through a simple inversion \( a(t) = 1/g(t) \). As a consequence, the outputs of multiplicative and divisive gain control can be qualitatively different.

Gain control in neural systems is ubiquitous (Shapley & Enroth-Cugell, 1984; Schwartz & Simoncelli, 2001); thus, it is important to understand its dynamics. For instance, what is the speed of adaptation for systems with gain control? Can we expect asymmetries in adaptation after stimulation with increments and decrements of the input (DeWeese & Zador, 1998; Snippe, Poot, & van Hateren, 2004; Hosoya, Baccus, & Meister, 2005)? Do systems with gain control have monotonic outputs when stimulated with simple monotonic inputs, or should we expect overshoots, undershoots, or oscillations in their output? By focusing on simple models for gain control,
we can start to answer these questions. Since gain control occurs at many levels in the neural system (Abbott, Varela, Sen, & Nelson, 1997; Salinas & Thier, 2000), the inputs \( I(t) \) in equations 1.1 and 1.2 are not necessarily sensory inputs; they could also represent the internal input to a process of gain control anywhere within the neural system.

The control signals \( g(t) \) in equation 1.1 and \( a(t) \) in equation 1.2 could be generated from either the input signal \( I(t) \) (feedforward control) or the output \( O(t) \) of the control loop (feedback control). In this letter, we concentrate on feedback control, since this appears to be the most common type of control in neural systems (Marmarelis, 1991; Torre, Ashmore, Lamb, & Menini, 1995; Calvert, Ho, Lefebvre, & Arshavsky, 1998; Crevier & Meister, 1998). A second reason to concentrate on feedback control is that the dynamics of a feedback loop is often less immediately obvious than the dynamics of a feedforward loop, especially when the control loop is nonlinear. Although the dynamics of linear, subtractive feedback control is well known (e.g., van de Vegte, 1990; Franklin, Powell & Emami-Naeini, 1994), less work has been done on the dynamics of multiplicative and divisive feedback control. Here we provide a mathematical analysis of such nonlinear feedback control.

The letter is organized as follows. In section 2, we define four feedback models—two with multiplicative control and the other two with divisive control. The structure of these models is simple—about as simple as possible for nonlinear feedback. This has been done on purpose, since it allows a mathematical analysis of the dynamics of these models rather than relying on numerical simulations. The results of this analysis should help to understand the behavior of more involved models that are too complex for an exact mathematical analysis. In section 3, we study the stability of the feedback models for a variety of inputs. In section 4, we study the dynamics of the control signals when the models are stimulated with step inputs, and in section 5, we show that these control signals can have strong asymmetries with respect to increment versus decrement steps in the input. In section 6, we focus on the output \( O(t) \) of the models rather than on the control signals \( g(t) \) and \( a(t) \). In particular, we investigate under what circumstances overshoots or oscillations in the output can occur when the models are stimulated with simple, monotonic inputs. Finally, in section 7 we restate the most important conclusions. To avoid disturbing the flow of the arguments, two appendixes contain longer mathematical derivations of the results.

2 Models

We analyze the dynamics of the four models for feedback control shown in Figure 1. Two of the models (\( M_{NL} \) and \( M_{LN} \); see Figure 1, top row) have a multiplicative gain control; the other two models (\( D_{NL} \) and \( D_{LN} \); see Figure 1, bottom row) have a divisive gain control. For each of the models,
Figure 1: Models for nonlinear feedback control. Models (A) $M_{NL}$ and (B) $M_{LN}$ have multiplicative control in which the output $O(t)$ equals the input $I(t)$ multiplied by a gain signal $g(t)$. Models (C) $D_{NL}$ and (D) $D_{LN}$ have divisive control in which the output $O(t)$ equals the input $I(t)$ divided by an attenuation signal $a(t)$. The feedback paths consist of a concatenation of a first-order low-pass filtering with time constant $\tau$ and an instantaneous nonlinearity ($f$ and $h$). Note that in models $M_{NL}$ and $D_{NL}$, the nonlinearity precedes the low-pass filtering in the feedback path, whereas in models $M_{LN}$ and $D_{LN}$, the low-pass filtering precedes the nonlinearity.

the control loop consists of a concatenation of an instantaneous nonlinearity (functions $f$ and $h$) and a linear low-pass filter $LP_{\tau}$ of first order with time constant $\tau$. For the two models on the left in Figure 1 ($M_{NL}$ and $D_{NL}$), the control loop consists of a nonlinearity followed by a low-pass filter $LP_{\tau}$, whereas for the two models on the right in Figure 1 ($M_{LN}$ and $D_{LN}$), the control loop consists of a low-pass filter $LP_{\tau}$, followed by a nonlinearity. Models of the general structure shown in Figure 1 have been shown to explain various aspects of processing in the visual system. For instance, Crevier and Meister (1998) analyzed a multiplicative feedback model of the type of Figure 1B to account for period doubling in the electroretinogram response to periodic flashes. A spatiotemporal extension of this model (Berry, Brivanlou, Jordan, & Meister, 1999) explained retinal responses of salamanders and rabbits to flashed and moving bars (see also Wilke et al., 2001). Snippe et al. (2004) showed that divisive feedback models of a type similar to Figure 1C can explain the asymmetric dynamics of gain control after increments and decrements of contrast. Divisive feedback has also been used to model the dynamics of adaptation in the auditory system (Dau, Püschel, & Kohlrausch, 1996). For simplicity, in the analysis of the models in...
Figure 1, we assume that the inputs $I(t)$ are nonnegative: $I(t) \geq 0$. This is reasonable, for example, for models of light adaptation in which the input signal (luminance) is nonnegative. To describe contrast-gain control (e.g., Berry et al., 1999), the input signal $I(t) = C(t)s(t)$ can be written as the product of a carrier signal $s(t)$ and a contrast envelope $C(t)$, with $C(t) \geq 0$. Because the carrier signal $s(t)$ can be negative, the input $I(t)$ does not satisfy $I(t) \geq 0$ in this case. However, for contrast-gain control, the effects of the carrier $s(t)$ are expected to be largely demodulated in the control loop (Snippe, Poot, & van Hateren, 2000). Thus, the dynamics of the control loop is governed mainly by the dynamics of the contrast envelope $C(t)$, which does satisfy nonnegativity: $C(t) \geq 0$. Hence, also for contrast-gain control, the assumption that the input is nonnegative is not a severe restriction.

Due to the first-order filtering in the models of Figure 1, the dynamics of these models are described by first-order differential equations. (See van Hateren, 2005, for a discussion on low-pass filtering in biological systems, and examples of biochemical processes that can be described as low-pass filters.) In general, the output $y(t)$ of a first-order low-pass filter with time constant $\tau$ is related to the input $x(t)$ to the filter through a first-order differential equation $\tau \frac{dy}{dt} = x - y$ (Oppenheim, Willsky, & Young, 1983). Thus, the dynamics of the gain signal $g(t)$in model $M_{NL}$ (see Figure 1A) is described by the first-order differential equation,

$$\tau \frac{dg}{dt} = f(O) - g = f(gI) - g,$$

(2.1)

since the input to the low-pass filter in the control loop of model $M_{NL}$ is $f(O)$, and the argument $O$ of the nonlinearity $f$ equals $gI$, due to the multiplicative nature of the gain control of model $M_{NL}$. Note that due to this multiplicative operation, equation 2.1 is a nonlinear differential equation even when the function $f$ is linear. The dynamics of the gain signal $g(t)$ for a given input $I(t)$ is obtained by solving equation 2.1 (either analytically or numerically). From the solution $g(t)$ for the gain, the output $O(t)$ can be obtained through $O(t) = g(t)I(t)$. When the input $I$ is constant, $I = I_s$, the system attains its steady state, $g = g_s$ and $O = O_s$. The input-output relation for the steady state can be obtained by setting the time derivative $\frac{dg}{dt}$ in equation 2.1 equal to zero, yielding $g_s = f(O_s)$. With $O_s = g_s I_s$, hence $g_s = O_s / I_s$, this yields the steady-state relation $O_s / I_s = f(O_s)$, hence $I_s = O_s / f(O_s)$. To obtain a system in which the dynamic range of $O_s$ is reduced relative to the dynamic range of $I_s$, we require that the steady-state gain $g_s = f(O_s)$ is a decreasing function of its argument, that is, the function $f(x)$ must satisfy $df(x)/dx < 0$. Note that this requirement is sufficient to guarantee a monotonic steady-state relation $I_s = O_s / f(O_s)$: with increasing $O_s$, $f(O_s)$ decreases, hence $I_s$ increases.
For model $D_{NL}$ (see Figure 1C), the dynamics of the attenuation signal $a(t)$ is described by the differential equation

$$\tau \frac{da}{dt} = h(O) - a = h(1/a) - a. \quad (2.2)$$

From the solution $a(t)$ of equation 2.2 for a given input $I(t)$, the output $O(t)$ of model $D_{NL}$ is obtained as $O(t) = I(t)/a(t)$. In steady state ($da/dt = 0$), equation 2.2 yields $a_s = h(O_s)$. With $O_s = I_s/a_s$, hence $a_s = I_s/O_s$, this gives the steady-state relation $I_s = O_s h(O_s)$. To obtain a reduction of the dynamic range of $O_s$ relative to the dynamic range of $I_s$, we require that the steady-state attenuation $a_s = h(O_s)$ is an increasing function of its argument, that is, $dh(x)/dx > 0$. This guarantees a monotonic steady-state relation $I_s = O_s h(O_s)$. Note that this steady-state relation becomes identical to that of the multiplicative model $M_{NL}$ when the nonlinearities $f(O)$ of model $M_{NL}$ and $h(O)$ of model $D_{NL}$ are related as $h(O) = 1/f(O)$.

A differential equation that describes the dynamics of model $M_{LN}$ (see Figure 1B) can be obtained for the output $\gamma(t)$ of the low-pass filter $LP_\tau$ in the feedback loop,

$$\tau \frac{d\gamma}{dt} = O - \gamma = gI - \gamma = f(\gamma)I - \gamma, \quad (2.3)$$

because the gain $g$ is related to $\gamma$ as $g = f(\gamma)$. From the solution $\gamma(t)$ of equation 2.3 for a given input $I(t)$, one obtains the dynamic gain $g(t)$ as $g(t) = f(\gamma(t))$, and thus the output $O(t) = g(t)I(t)$. In steady state ($d\gamma/dt = 0$), equation 2.3 yields $\gamma_s = O_s = f(O_s)I_s$, hence $I_s = O_s/f(O_s)$, which is identical to the steady-state behavior of model $M_{NL}$. As in model $M_{NL}$, for model $M_{LN}$ we require that $f$ be a decreasing function of its argument.

Finally, the dynamics of model $D_{LN}$ (see Figure 1D) follows from the differential equation for the output $\alpha(t)$ of the low-pass filter in model $D_{LN}$:

$$\tau \frac{d\alpha}{dt} = O - \alpha = \frac{I}{a} - \alpha = \frac{I}{h(\alpha)} - \alpha. \quad (2.4)$$

From the solution $\alpha(t)$ of this differential equation, one obtains the attenuation $a(t) = h(\alpha(t))$, and thus the output $O(t) = I(t)/a(t)$. In steady state ($d\alpha/dt = 0$), equation 2.4 produces the steady-state input-output relation $I_s = O_s h(O_s)$, which is identical to the steady-state equation obtained for model $D_{NL}$. As in model $D_{NL}$, we require that $h$ be an increasing function of its argument.
2.1 The Nonlinearities $f(x)$ and $h(x)$ Need Not Be Positive for All $x$. Although for simplicity we assumed that the input $I$ is nonnegative, $I \geq 0$, a similar assumption for the nonlinearities $f$ and $h$ in the feedback loops of the models in Figure 1 would be too restrictive, since this would leave out viable and interesting models for gain control. Thus, we allow the functions $f(x)$ in multiplicative control and $h(x)$ in divisive control to be negative for certain ranges of their argument $x$. Since $f(x)$ is assumed to be decreasing, this means that we allow functions $f(x)$ that are positive in a range $0 < x < x_0$, become zero at $x = x_0$, and are negative for $x > x_0$, with $df/dx < 0$ over the entire range $0 < x < \infty$. An example of such a function $f$ would be a linearly decreasing function $f(x) = k(x_0 - x)$, with $k$ and $x_0$ positive constants. For a linear function $f(x)$, the ordering of $f$ and the low-pass filtering in Figure 1 is arbitrary, and models $M_{NL}$ and $M_{LN}$ become identical. Solving the steady-state relation $I_s = O_s/f(O_s)$ with respect to $O_s$ for this $f$ yields $O_s = x_0kI_s/(1 + kI_s)$, a Naka-Rushton relationship (Heeger, 1992). Note that $x_0$ represents the largest steady-state output $O_s$ that can be obtained in this case and that $f(O_s) \geq 0$ for all steady inputs $I_s$. In a dynamic situation, however, after sudden increases in the input $I(t)$, the output $O(t)$ can become larger than $x_0$, and $f(O)$ is temporarily negative. This negative value of the function $f$ helps to quickly reduce the gain $g$ (through equation 2.1), which reduces the output $O$ back to values below $x_0$. A comparison of the dynamics of adaptation of such a multiplicative feedback system (with $k = x_0 = 1$) after increments and decrements of the input is shown in Figure 2A. Note that despite the linearity of $f$, the dynamics is asymmetric for increments versus decrements. Allowing negative values for $f(x)$ in multiplicative control can thus be beneficial in that it speeds up adaptation after increases in $I(t)$. Nevertheless, in comparing multiplicative and divisive control, some care is required when we allow $f(x)$ in multiplicative control to be zero for $x = x_0$ and negative for $x > x_0$. This means that the corresponding $h(x) = 1/f(x)$ in divisive control is monotonically increasing up to $x = x_0$, where it becomes infinite. For $x > x_0$, $h(x)$ becomes negative, and thus $h(x)$ is nonmonotonic in the range $0 < x < \infty$. For model $D_{LN}$ (see Figure 1D), this is actually not a problem, since for this model, $x < x_0$ also in dynamic situations. An example of adaptation for such a model $D_{LN}$ (again with a Naka-Rushton steady state) is shown in Figure 2B. On the other hand, for model $D_{NL}$ (see Figure 1C), the discontinuity in the function $h(x)$ could become a problem for strong increments at the input. The solution to this problem is to assume that the output $O(t)$ for a divisive control system with such an $h(x)$ in the feedback path remains smaller than $x_0$ also in dynamic situations, so $h(x)$ remains positive at all $t$. It can be shown that this is indeed what happens when the input $I(t)$ to the system is a continuous function of time, as will always be the case in practice. An example of adaptation in such a model $D_{NL}$ (again with a Naka-Rushton steady state) is shown in Figure 2C. Note the strong asymmetry of the dynamics of this model for increments versus decrements of the input.
Figure 2: (A) Dynamics of the gain \( g(t) \) in a multiplicative feedback control (with time constant \( \tau = 1 \)) with a linear function \( f(x) = 1 - x \) in the feedback path, which yields a Naka-Rushton relation \( O_s = I_s/(1 + I_s) \) for the steady state. The solid line is \( g(t) \) in response to an increment step of \( I \) (from \( 1/4 \) to 4). The dashed line is \( g(t) \) after a decrement step of \( I \) (from 4 to \( 1/4 \)). For linear \( f(x) \), models \( M_{NL} \) and \( M_{LN} \) are identical. (B) Dynamics of the attenuation \( a(t) \) of model \( D_{LN} \) (see Figure 1D; \( \tau = 1 \)) when \( h(\alpha) = 1/(1 - \alpha) \), which yields a Naka-Rushton steady state \( O_s = I_s/(1 + I_s) \). Input steps are identical to A. (C) Dynamics of \( a(t) \) of model \( D_{NL} \) (see Figure 1C; \( \tau = 1 \)) when \( h(O) = 1/(1-O) \). Steady state of this model is identical to A and B, but the dynamics is very different. (D) Dynamics of \( a(t) \) of model \( D_{NL} \) (see Figure 1C; \( \tau = 1 \)) when \( h(O) = 1 - (1/O) \), which yields \( O_s = 1 + I_s \) in steady state.

Likewise, in divisive control we allow increasing functions \( h(x) \) that are negative for \( x < x_0 \) and positive for \( x > x_0 \). For such systems, steady-state output \( O_s \) is never smaller than \( x_0 \); hence, \( h(O_s) \geq 0 \). When \( I_s = 0 \), \( O_s = x_0 \). Thus, for such systems, \( x_0 \) can be thought of as a spontaneous activity. After large decrements of \( I(t) \), the output \( O(t) \) can temporarily be smaller than this spontaneous activity \( x_0 \) of the system; hence, \( h(O) < 0 \), which speeds up adaptation according to equation 2.2. An example is shown in Figure 2D. For the corresponding multiplicative control, with \( f(x) = 1/h(x) \), \( f(O) \) becomes very large when the output \( O \) approaches the spontaneous
activity $x_0$, and for continuous inputs $I(t)$, this effect is sufficiently strong to keep $O(t) > x_0$ at all times $t$.

2.2 Identity of Models $M_{LN}$ and $D_{LN}$. Equations 2.3 and 2.4 yield identical dynamics when the nonlinearities $f$ in equation 2.3 and $h$ in equation 2.4 are related as $h = 1/f$. This simply says that multiplying an input $I$ with a gain $g$ to obtain an output $O = gI$ is identical to dividing $I$ by the inverse gain (attenuation) $1/g : O = I/[1/g]$. Thus, when the nonlinear functions $f$ and $h$ are related as $h = 1/f$, model $M_{LN}$ and model $D_{LN}$ in Figure 1 yield identical responses if they are stimulated with the same inputs. Figures 2A and 2B provide an example: the dynamic attenuation $a(t)$ of model $D_{LN}$ in Figure 2B equals the inverse of the dynamic gain $g(t)$ of model $M_{LN}$ in Figure 2A, that is, $a(t) = 1/g(t)$.

2.3 Duality of Models $M_{NL}$ and $D_{NL}$. Likewise, models $M_{NL}$ and $D_{NL}$ are closely related, but in this case, the relationship amounts to a duality rather than an identity. For the duality, the nonlinearities $f$ in equation 2.1 and $h$ in equation 2.2 have to be related through an inversion of their argument: $h(x) = f(1/x)$. In that case, when model $D_{NL}$ is stimulated with an input $I_D(t) = 1/I_M(t)$ that is the inverse of the input $I_M(t)$ to model $M_{NL}$, the dynamics 2.2 for the attenuation $a(t)$ becomes

$$\tau \frac{da}{dt} = h(I_D/a) - a = f(a/I_D) - a = f(I_Ma) - a,$$

(2.5)

which is identical to the dynamics of $g(t)$ in equation 2.1. Thus, under these conditions, the dynamic attenuation $a(t)$ of model $D_{NL}$ equals the dynamic gain $g(t)$ of model $M_{NL}: a(t) = g(t)$. Then the output $O_D(t)$ of model $D_{NL}$ is related to the output $O_M(t)$ of model $M_{NL}$ through an inversion: $O_D = I_D/a = 1/[I_Mg] = 1/O_M$. Figures 2A and 2D provide an example of this duality of models $D_{NL}$ and $M_{NL}$. The attenuation $a(t)$ in Figure 2D after an increment step of the input $I$ (from $1/4$ to 4) equals the gain $g(t)$ in Figure 2A after a decrement step of $I$ (from 4 to $1/4$). Likewise, $a(t)$ in Figure 2D after a decrement step of $I$ equals $g(t)$ after an increment step in Figure 2A. Thus, when the nonlinearities $f$ and $h$ are related through an inversion of their argument, $h(x) = f(1/x)$, the models $M_{NL}$ and $D_{NL}$ are dual in the following sense: when model $M_{NL}$ transforms an input $I(t)$ into an output $O(t)$, model $D_{NL}$ will transform the input $1/I(t)$ into the output $1/O(t)$. Of course, the duality also works in the other direction, from model $D_{NL}$ to model $M_{NL}$. Apart from the theoretical interest of this duality between multiplicative and divisive control, the duality can be useful in applications. When the mathematics or the statistics of $1/I(t)$ are simpler than those of the input $I(t)$ itself, it makes sense to do the calculations in the dual model. Stimulating the dual model with an input $1/I(t)$ and inverting the resulting output of the dual model yields the output $O(t)$ of the original model.
3 Stability

As is well known, feedback can lead to instabilities (Bechhoefer, 2005). Here we show that this is not the case for the feedback systems studied in this letter. The basic reason for this is that the low-pass filters in the feedback loops of the schemes in Figure 1 are first order, that is, they are described by the first-order differential equations 2.1 to 2.4. A first-order low-pass filter has an exponential pulse response that starts to operate as soon as a disturbance occurs, that is, without a delay, which could yield instabilities (Bechhoefer, 2005).

3.1 The Models Are Stable for Constant Input. To see more formally that the feedback schemes studied in this letter are stable, first assume that the input signal \( I(t) \) is constant, \( I(t) = I_s \). For model \( M_{NL} \), the corresponding steady-state gain \( g_s \) is obtained by setting the time derivative \( dg/dt \) in equation 2.1 to zero; hence, \( f(g, I_s) - g_s = 0 \). Now assume that at some moment, the actual gain \( g \) is larger than the steady-state gain \( g_s \), \( g > g_s \). Since the function \( f \) is a decreasing function of its argument, we have \( f(g, I_s) < f(g_s, I_s) \), and therefore \( f(g, I_s) - g < f(g_s, I_s) - g_s = 0 \). Hence, it follows from equation 2.1 that \( dg/dt < 0 \). Thus, \( g \) will decrease from its initial value (which is larger than \( g_s \)) toward the steady-state value \( g_s \). Likewise, when \( g \) is initially smaller than \( g_s \), \( g \) will increase toward the steady-state value \( g_s \). Hence, for a constant input \( I \), any deviations from steady state will always decrease over time; that is, for constant input \( I \), the model \( M_{NL} \) is stable. Similar reasoning shows that for constant input, the other models in Figure 1 are also stable.

3.2 The Models Are Stable for Arbitrary, Bounded Input. Now assume that the input \( I(t) \) is not necessarily constant, but that it is bounded, say, between a lower bound \( I_- \) and an upper bound \( I_+ \), that is, at all times \( t : I_- \leq I(t) \leq I_+ \). For such bounded inputs, the systems studied here cannot become unstable; their control signals (and hence their outputs) will remain finite. For instance, consider model \( D_{NL} \), in which the dynamics of the control (attenuation) signal \( a \) is described by equation 2.2. Now take any moment \( t_0 \) in time. At that moment, the input to the system is \( I_0 = I(t_0) \), to which corresponds a steady-state value \( a_s \) for which (from equation 2.2) \( h(I_0/a_s) - a_s = 0 \). Assume that at the moment \( t_0 \), the actual control signal \( a(t_0) \) is larger than this steady-state value \( a_s \). Then, since the function \( h(x) \) is an increasing function of its argument \( x \), and hence \( h(1/a) \) decreases with increasing \( a \), we can be sure that when \( a > a_0, h(I_0/a) - a < h(I_0/a_s) - a_s = 0 \). Thus, from equation 2.2, \( da/dt < 0 \), that is, an attenuation signal that is too large (relative to the instantaneous steady state) is guaranteed to decrease. Similarly, if at any moment the attenuation signal \( a \) is too small (relative to the instantaneous steady state), it will increase. In particular, if at some initial time \( t_0 \) the attenuation signal \( a \) would be larger than the
steady-state value $a_{s+}$ corresponding to the upper bound $I_+$, $a(t)$ is guaranteed to decrease monotonically until it becomes smaller than $a_{s+}$. Likewise, if at time $t_0$ the attenuation signal $a$ is smaller than the steady-state value $a_{s-}$ corresponding to the lower bound $I_-$, $a(t)$ will increase monotonically until it becomes larger than $a_{s-}$. And if initially $a_{s-} < a(t_0) < a_{s+}$, then $a_{s-} < a(t) < a_{s+}$ for all times $t > t_0$. Figure 3 illustrates this behavior for a specific choice of the nonlinearity, $h(x) = x^2$.

3.3 Monotonic Input Yields Monotonic Control Signals. The reasoning we used above to demonstrate the stability of the feedback schemes of Figure 1 can also be used to derive general qualitative properties of the control signals in these schemes. For instance, assume that the input $I(t)$ is a monotonically increasing function of time for times $t > t_0$ and that at time $t_0$, the attenuation signal $a(t_0)$ of model $D_{NL}$ is not larger than the steady-state level $a_s$ corresponding to the input $I(t_0)$, $a(t_0) \leq a_s$. Then we can be sure that the divisive control signal $a(t)$ is also monotonically increasing, without any overshoots or oscillations. If $a(t)$ would be nonmonotonic, there would be times $t_1 > t_0$ for which $da/dt < 0$. According to equation 2.2, this means that at that time $t_1$, the attenuation signal has to be larger than the steady-state corresponding to the input $I(t_1)$ at time $t_1$. But this means that $a(t)$ must have crossed its steady state at some moment $t$ between $t_0$ and $t_1$. But at that hypothetical moment, according to equation 2.2, $da/dt = 0$. Thus, a crossing of $a(t)$ with its instantaneous steady-state value $a_s(t)$ would be possible.

Figure 3: Stability of feedback control. Different initial values for the control signal (dashed lines) converge to identical solutions. Shown is an example of model $D_{NL}$, with $h(O) = O^2$ and $\tau = 3$. Input $I(t) = I(1 + \sin \omega t)$, with $I = \omega = 1$. For constant input $I(t) = I_s$, steady-state attenuation $a_s = I_s^{2/3}$ in this model. The continuous line is a plot of the instantaneous steady state $a_s(t) = (I(t))^{2/3}$, which can be compared with the dynamics of the actual attenuation $a(t)$. Note that $da/dt < 0$ when $a$ is above the instantaneous steady state, $da/dt > 0$ when $a$ is below steady state, and $da/dt = 0$ whenever $a(t)$ crosses steady state.
Figure 4: Attenuation $a(t)$ (dashed line) of the model of Figure 3, when $I(t)$ is monotonic (a series of steps in this example). The attenuation cannot overshoot its steady-state solution $a_s = I^{2/3}$ (continuous line), since $da/dt$ becomes 0 when $a$ approaches steady state. Hence, when $a(t)$ is initially below this line, it cannot escape from the region below the continuous line. Since $da/dt > 0$ when $a < a_s$, a monotonic input $I(t)$ yields a monotonic control signal $a(t)$.

only if $dI/dt < 0$ at that moment (as can be observed in Figure 3), contrary to the assumption of a monotonically increasing $I(t)$. Figure 4 illustrates the behavior of $a(t)$ for a specific choice of $I(t)$ and the nonlinearity $h$, but the conclusion is general. For the systems in Figure 1, monotonic inputs $I(t)$ yield control signals $a(t)$, respectively $g(t)$, that are monotonic; they do not overshoot or oscillate.

4 Speed of Adaptation After Steps in the Input

Here we look at the speed of adaptation of the models in Figure 1 immediately after a step in the input $I(t)$. Steps in the input occur in natural stimuli (e.g., Griffin, Lillholm, & Nielsen, 2004) and are often used to study the dynamics of adaptation (e.g., Crawford, 1947; Thorson & Biederman-Thorson, 1974; Snippe et al., 2000; Fairhall, Lewen, Bialek, & de Ruyter van Steveninck, 2001; Rieke, 2001). Without loss of generality, the moment of the step in the input is chosen as $t = 0$. For an increment step, the input at $t = 0$ switches from a value $I_-$ to a higher value $I_+ > I_-$. We assume that for $t < 0$, the input has been at $I_-$ for a sufficiently long time such that at time $t = 0$, the system is in the steady state corresponding to input $I_-$, that is, the system is fully adapted to $I_-$. When the input step at $t = 0$ occurs, the system starts to adapt to the new input $I_+$. Likewise, for a decrement step $I_+ \rightarrow I_-$ at time $t = 0$, we assume that at $t = 0$, the system is fully adapted to the input $I_+$. We compare the initial speed of adaptation for the models in Figure 1 immediately after increment steps $I_- \rightarrow I_+$ and decrement steps $I_+ \rightarrow I_-$. Speed of adaptation is quantified using equations 2.1 to 2.4, which
give the speed with which the control loops in Figure 1 adjust after the step in the input.

4.1 Comparison of Multiplicative and Divisive Control

4.1.1 Models $M_{LN}$ and $D_{LN}$ Have Identical Dynamics. As noted in section 2.2, the multiplicative model $M_{LN}$ in Figure 1B and the divisive model $D_{LN}$ in Figure 1D become identical when the nonlinearities $f$ and $h$ in the control paths are related as $h = 1/f$. When $f$ and $h$ are related in this way, the attenuation signal $a(t)$ in model $D_{LN}$ is identical to the inverse $1/g(t)$ of the gain signal $g(t)$ in model $M_{LN}$. Thus, the dynamics of $a(t)$ and $1/g(t)$ are identical: $\frac{da}{dt} = \frac{1}{g(t)}$, which means that the speed of adaptation in models $M_{LN}$ and $D_{LN}$ is identical.

4.1.2 Large Differences in Dynamics for Models $M_{NL}$ and $D_{NL}$. We find large differences when we compare adaptation in models $M_{NL}$ (see Figure 1A) and $D_{NL}$ (see Figure 1C) in which the nonlinearities $f$, respectively $h$, precede the low-pass filtering in the feedback loop. It is still the case that we can equate the steady-state behavior of models $M_{NL}$ and $D_{NL}$ by choosing $h = 1/f$, which yields $a_s = 1/g_s$. However, even in this case, $a(t)$ and $1/g(t)$ immediately after the step in the input $I(t)$ are different. For model $D_{NL}$, the dynamics of $a(t)$ is given by equation 2.2. For model $M_{NL}$, the dynamics of $g(t)$ is given by equation 2.1, which yields for the inverse gain $1/g(t)$ immediately after the step in $I(t)$:

$$
\tau \frac{d[1/g]}{dt} = -\tau \frac{dg}{(g_s)^2 dt} = \frac{1}{g_s} - \frac{f(g_s I)}{(g_s)^2} = a_s - \frac{(a_s)^2}{h(1/a_s)},
$$

(4.1)

in which we used the relation $f = 1/h$, and the fact that immediately after the step in $I(t)$, the gain $g$ and the attenuation $a$ still have their steady-state value, and hence are related as $g_s = 1/a_s$. Comparing result 4.1 with the result $\tau da/dt = h(1/a_s) - a_s$ of equation 2.2 immediately after a step in the input $I(t)$, we find

$$
\tau \frac{da}{dt} = h(1/a_s) - a_s \quad \frac{d[1/g]}{dt} = \frac{(a_s)^2}{h(1/a_s)}[h(1/a_s) - a_s]^2.
$$

(4.2)

After an increment step in $I(t)$ (when $da/dt$, $d[1/g]/dt$ and $h(1/a_s)$ are all positive), it follows from equation 4.2 that $da/dt > d[1/g]/dt$. Thus, immediately after an increment step of the input, adaptation in the divisive feedback model $D_{NL}$ is faster than adaptation in the multiplicative feedback model $M_{NL}$. In fact, this is true not only immediately after the increment step, but also at later times $t$, in the sense that for all $t > 0$, $a(t) > 1/g(t)$. 

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Thus, after an increment step, the multiplicative gain control never catches up with the divisive gain control. The proof of this assertion is easy: suppose that at some time \( t = t^* \), the multiplicative control would have just caught up with the divisive control, that is, suppose that at \( t = t^* \), \( a(t^*) = 1/g(t^*) \), with \( a(t) > 1/g(t) \) for \( 0 < t < t^* \). Then it follows from equation 4.2 evaluated at \( t = t^* \) that \( da/dt > d[1/g]/dt \) immediately before \( t = t^* \); thus, \( a < 1/g \) immediately before \( t = t^* \). This contradicts the original assertion that \( a(t) > 1/g(t) \) for \( 0 < t < t^* \); hence \( a(t) > 1/g(t) \) for all \( t > 0 \). Thus, after an increment step in \( I(t) \), adaptation in the divisive control system \( D_{NL} \) is consistently faster than adaptation in the multiplicative control system \( M_{NL} \). On the other hand, after a decrement step in \( I(t) \) (when both \( da/dt \) and \( d[1/g]/dt \) are negative), equation 4.2 yields \( |d[1/g]/dt| > |da/dt| \), assuming that \( h(1/a_s) > 0 \) after the step. In fact, the assumption \( h(1/a_s) > 0 \) is not really needed in this case, since we argued in section 2.1 that when \( h(x) \) becomes negative in a divisive control, the gain \( g \) in the corresponding multiplicative control with \( f(x) = 1/h(x) \) changes very rapidly in order to keep the output \( O(t) \) in its required range; hence, \( |d[1/g]/dt| > |da/dt| \) also when \( h(1/a_s) < 0 \). Thus, after a decrement step, adaptation in the multiplicative model \( M_{NL} \) is faster than adaptation in the divisive model \( D_{NL} \). An example is given in Figure 5 using a quadratic nonlinearity \( h(O) = O^2 \) for the divisive control and hence \( f(O) = 1/h(O) = 1/O^2 \) for the multiplicative control, with identical time constant \( \tau \) of the low-pass filtering in the control loops. The example shows that the differences in speed of adaptation between multiplicative and divisive control can be large.

4.2 The Order of the Nonlinearity and the Low-Pass Filtering in the Feedback Can Have Strong Effects. In the previous section, we showed
that the dynamics of divisive and multiplicative control can be very different, even under conditions where the steady-state behaviors of these systems are identical. Here we show that also for a specific choice of control, either divisive or multiplicative, the order of the two operations, nonlinearity and low-pass filtering, in the feedback loops of Figure 1 can have a strong effect on the dynamics of the control system.

First, we look at divisive gain control, and compare model $D_{NL}$ (Figure 1C) in which the nonlinearity $h$ precedes the low-pass filtering in the feedback loop with model $D_{LN}$ (Figure 1D) in which the nonlinearity $h$ occurs after the low-pass filtering. If the function $h(x)$ is linear, $h(x) = c + kx$, models $D_{NL}$ and $D_{LN}$ are identical, since the order of two linear operations (here, low-pass filtering and $h(x) = c + kx$) has no effect on the outcome. Thus, for linear $h(x)$, models $D_{NL}$ and $D_{LN}$ have identical dynamics. This, however, is not the case when $h(x)$ is nonlinear. As will be argued below, in that case, the speed of adaptation of model $D_{NL}$ relative to model $D_{LN}$ is determined by the curvature of $h(x)$, that is, by its second-order derivative $d^2h(x)/dx^2$. If $h(x)$ is an expansive function of $x$ (i.e., if it has a positive second-order derivative everywhere), adaptation after an increment step $I_- \rightarrow I_+$ is faster in model $D_{NL}$ than in model $D_{LN}$. For model $D_{NL}$, speed of adaptation is governed by equation 2.2; immediately after the increment step,

$$
\tau \frac{da}{dt} = h(I_+/a_+) - a_+ = h(I_+/a_-) - h(I_-/a_-) \quad \text{(Model } D_{NL})
$$

where $a_-$ is the steady-state attenuation corresponding to input $I_-$. and we have used the fact that in steady state, $a_- = h(I_-/a_-)$. On the other hand, for model $D_{LN}$, adaptation is governed by equation 2.4, which for the attenuation signal $a = h(\alpha)$ yields

$$
\tau \frac{da}{dt} = \left[ \frac{dh(x)}{dx} \right]_{x = I_+/a_-} \cdot \tau \frac{d\alpha}{dt} = \left[ \frac{dh(x)}{dx} \right]_{x = I_-/a_-} \cdot \left( \frac{I_+}{a_-} - \alpha_- \right) \quad \text{(Model } D_{LN})
$$

where in the last step, we used the fact that in steady state, $\alpha_- = I_-/a_-$. Because of the factor $dh/dx$ in equation 4.4, adaptation in model $D_{LN}$ is governed by a linear extrapolation of the function $h(x)$. As illustrated in Figure 6, for an expansive function $h(x)$, that is, when $d^2h(x)/dx^2 > 0$, the outcome of equation 4.3 is larger than the outcome of equation 4.4. Thus, immediately after an increment step, adaptation in model $D_{NL}$ is faster than in model $D_{LN}$. The intuition for this difference in behavior of the two models is that in model $D_{NL}$, the overshoot in the output $O(t)$ immediately after the increment is accentuated by an expansive function $h(O)$, which
immediately after the input increment

Figure 6: Comparison of adaptation in models $D_{NL}$ and $D_{LN}$ immediately after an increment step $I_\rightarrow I_+$ of the input. For model $D_{NL}$, the dynamics of adaptation immediately after the step is governed by the difference of the values of the nonlinearity $h(O)$ at the outputs before and after the input step. For model $D_{LN}$, the dynamics of adaptation immediately after the step is governed by a linear extrapolation of $h$ (dotted line). When, as in this example, the function $h(O)$ has positive curvature, adaptation after an increment step is faster in model $D_{NL}$ than in model $D_{LN}$.

provides a powerful drive to the low-pass filter, and hence fast adaptation. As in section 4.1, it is easy to prove that the difference in adaptation persists for all $t > 0$; after an increment step in the input, adaptation in model $D_{NL}$ is consistently faster than adaptation in model $D_{LN}$ when $h(x)$ is expansive. On the other hand, when $h(x)$ is compressive, that is, when $d^2 h(x)/dx^2 < 0$, the linear extrapolation of equation 4.4 exceeds the result of equation 4.3, and adaptation in model $D_{LN}$ after an increment step is faster than adaptation in model $D_{NL}$. After a decrement step $I_+ \rightarrow I_-$, it works just the other way around: when $h(x)$ is expansive, adaptation in model $D_{LN}$ is faster than in model $D_{NL}$, and when $h(x)$ is compressive, adaptation in model $D_{NL}$ is faster than in model $D_{LN}$.

For multiplicative gain control, similar results hold when comparing adaptation in model $M_{NL}$ (see Figure 1A) with adaptation in model $M_{LN}$ (see Figure 1B). Models $M_{NL}$ and $M_{LN}$ are identical in their dynamics when $f(x)$ is a linear function $f(x) = d - kx$ (with $k > 0$ to obtain range compression). When $f(x)$ is a nonlinear function, the dynamics of adaptation in models $M_{NL}$ and $M_{LN}$ differ, and again the sign of the difference in speed of adaptation is governed by the curvature of $f(x)$, that is, by its second-order derivative $d^2 f(x)/dx^2$. If $d^2 f(x)/dx^2 > 0$, adaptation after an increment step $I_- \rightarrow I_+$ is faster in model $M_{LN}$ than in model $M_{NL}$, whereas after a decrement step $I_+ \rightarrow I_-$, adaptation is faster in model $M_{NL}$ than in model $M_{LN}$. Figure 7 gives an example and shows that the difference in speed of adaptation can be substantial. If $d^2 f(x)/dx^2 < 0$, the situation
Figure 7: Comparison of adaptation in model $M_{NL}$ (dashed lines) and model $M_{LN}$ (dotted lines) when the nonlinearity in the feedback loop $f(x) = 1/x^2$ and $\tau = 3$. The input $I(t)$ is an increment step from 1 to 8 (A) and a decrement step from 8 to 1 (B). Note that models $M_{NL}$ and $M_{LN}$ have identical steady state $g_s = I^{-2/3}$ (continuous lines) but strongly different dynamics.

reverses, and adaptation after an increment step is faster in model $M_{NL}$ than in model $M_{LN}$, whereas adaptation after a decrement step is faster in model $M_{LN}$ than in model $M_{NL}$.

5 Asymmetries of Adaptation After Increments and Decrements of the Input

In a linear system, responses after increments and decrements of the input are equally fast. The systems we study here, however, are fundamentally nonlinear, and the speed with which they adapt to increment steps can be strongly different from the speed with which they adapt to decrement steps. For the models of Figure 1, such strong asymmetries of adaptation can be observed in Figures 5 and 7 by comparing the different panels. For contrast gain control, adaptation for an ideal observer has been predicted to be faster after increments of contrast than after decrements of contrast (DeWeese & Zador, 1998). This prediction has been confirmed for human subjects (Snippe & van Hateren, 2003; Snippe et al., 2004). This type of asymmetry can be observed in Figure 5 for model $D_{NL}$ and in Figure 7 for model $M_{LN}$. Similarly, faster adaptation after contrast increments than after decrements has been found in ganglion cells of salamanders and rabbits (Smirnakis, Berry, Warland, Bialek, & Meister, 1997), in salamander bipolar cells (Rieke, 2001), and in motion-sensitive cells in the visual system of the fly (Fairhall et al., 2001). Here we study these increment and decrement asymmetries for the models in Figure 1. For each of the models of Figure 1, the model will adapt faster to increment stimuli for some nonlinearities, in the feedback path, whereas for other nonlinearities, the model will adapt faster to decrement stimuli. However, despite their nonlinear nature, for
each of the models in Figure 1, there is a class of nonlinearities in the feedback path such that adaptation is initially equally fast after an increment step \( I_- \rightarrow I_+ \) and after a decrement step \( I_+ \rightarrow I_- \) of the input.

### 5.1 Increment and Decrement Symmetry for Model LN Is Obtained

When \( h(x) = c \exp(kx) \). For model LN (see Figure 1D), the speed of adaptation immediately after an increment step \( I_- \rightarrow I_+ \) of the input follows from equation 4.4; thus,

\[
\tau \frac{da}{dt} = \tau \frac{dh(\alpha)}{d\alpha} = \tau \frac{dh(\alpha)}{d\alpha} \frac{d\alpha}{dt} = \frac{dh(\alpha)}{d\alpha} \left[ O - \alpha \right] = \frac{dh(\alpha)}{d\alpha} \left[ \frac{I_+}{h(\alpha)} - \frac{I_-}{h(\alpha)} \right]
\]

\[
= \frac{d \ln h(\alpha)}{d\alpha} \left[ I_+ - I_- \right].
\]

(5.1)

In the last step of equation 5.1 we have used the equality \((1/h(x))dh(x)/dx = d \ln h(x)/dx\), and this derivative is evaluated at the steady-state value of \( \alpha \) corresponding to the input \( I_- \) before the increment step. After a decrement step \( I_+ \rightarrow I_- \), a similar derivation as in equation 5.1 shows that the speed of adaptation immediately after the step follows from \( \tau da/dt = d \ln h(\alpha)/d\alpha \left[ I_- - I_+ \right] \), where the derivative \( d \ln h(\alpha)/d\alpha \) is now evaluated at the steady-state value of \( \alpha \) corresponding to the input \( I_+ \) before the decrement step. Thus, in model LN, the speed of adaptation \( da/dt \) immediately after increment and decrement steps will be identical (except for the sign, \( [I_+ - I_-] \) versus \( [I_- - I_+] \)) if the derivative \( d \ln h(\alpha)/d\alpha \) is identical at the points \( \alpha \) corresponding to steady-state at input \( I_- \), respectively, \( I_+ \). This will be the case for any pair of values \( I_+, I_- \) of the input \( I \) if the nonlinearity \( h(x) \) is such that \( d \ln h(x)/dx = k \), a constant (which must be chosen positive to obtain gain control), hence \( \ln h(x) = kx + \ln c \), with \( c \) another positive constant. Thus, for model LN, an exponential nonlinearity \( h(x) = c \exp(kx) \) will yield equally fast adaptation immediately after increment and decrement steps. Due to the nonlinear nature of the model, this equality will not hold for adaptation at later times after the steps, but still it is remarkable that for this nonlinear model, there is a unique shape of the nonlinearity \( h(x) \) (i.e., an exponential) that yields symmetric increment and decrement adaptation immediately after the steps for any pair \( I_+, I_- \) of input levels. Moreover, the structure of equation 5.1 for adaptation immediately after steps in the input leads to a simple rule for the sign of any increment or decrement asymmetries of adaptation in model LN when \( h(x) \) is not an exponential function: the critical feature of \( h(x) \) is the behavior of \( d \ln h(x)/dx \) as a function of \( x \). If \( d \ln h(x)/dx \) increases with \( x \) (i.e., when \( \ln h(x) \) is an expansive function, \( d^2 \ln h(x)/dx^2 > 0 \)), adaptation immediately after a decrement step will be faster than adaptation after an increment step. This is because when \( \ln h(x) \) is expansive, \( d \ln h(x)/dx \) will be larger (hence, adaptation faster, according to equation 5.1) at the high
steady-state level $x_+$ that is present immediately before a decrement step than at the low steady-state level $x_-$ that is present immediately before an increment step.

5.2 Increment and Decrement Symmetry for Model $MLN$ Is Obtained When $f(x) = \sqrt{c - kx}$. For model $MLN$ (see Figure 1B), the nonlinearity $f(x)$ governs (a)symmetry of adaptation after increments versus decrements. Using equation 2.3, speed of adaptation of the gain signal $g = f(γ)$ immediately after an increment step $I_+ → I_-$ in the input is

$$
\frac{d\tau}{dt} = \tau \frac{df(γ)}{dt} = \tau \frac{df(γ)}{dγ} \frac{dγ}{dt} = \frac{d[γf(γ)]}{dγ}[O - γ]
$$

$$
= \frac{d[γf(γ)]}{dγ}[f(γ)I_+ - f(γ)I_-] = \frac{1}{2} \frac{d[f(γ)]^2}{dγ}\left[I_+ - I_-, \right]
$$

(5.2)

with the derivative $d[f(γ)]^2/dγ$ evaluated at the steady-state value of $γ$ that corresponds to the input $I_-$ immediately before the input step. After a decrement step $I_- → I_+$, the speed of adaptation immediately after the step is minus the result 5.2, but with the derivative now evaluated at the steady state corresponding to $I_+$. Thus, the speed of adaptation immediately after increment and decrement steps is identical when $d[f(x)]^2/dx = -k$, a constant (the minus sign indicates that $k$ should be chosen positive to obtain multiplicative gain control). From this follows $[f(x)]^2 = c - kx$ (with $c$ another positive constant), hence $f(x) = \sqrt{c - kx}$. For other choices of $f(x)$, asymmetric adaptation of $g(t)$ occurs after increments versus decrements, and the sign of the asymmetry is governed by the curvature (i.e., the second-order derivative) of $[f(x)]^2$. If $[f(x)]^2$ has positive curvature (i.e., when $d^2[f(x)]^2/dx^2 > 0$), adaptation of $g(t)$ is faster after increment steps than after decrement steps, whereas the reverse holds when $[f(x)]^2$ has negative curvature.

Due to the identity of models $MLN$ and $DLN$ noted in section 2.1, the results derived above for model $DLN$ can be immediately translated into results for model $MLN$, and vice versa. For instance, symmetry of initial adaptation in the divisive model $DLN$ was obtained for a nonlinearity $h(x) = c \exp (kx)$, which corresponds to $f(x) = 1/h(x) = (1/c) \exp (-kx)$ in the equivalent multiplicative model $MLN$. Since $da/dt = \frac{d}{dt}(1/g)dt = -(1/g^2)dg/dt$, for this choice of $f(x)$, the speed of adaptation of the gain $g$ divided by the square of this gain is symmetric after increment and decrement steps of the input. Likewise, a choice $h(x) = 1/\sqrt{c - kx}$ leads to a divisive model $DLN$ in which $(1/a^2)da/dt$ is symmetric after increment and decrement steps. Finally, we ask if there is a nonlinearity $f(x) = 1/h(x)$ such that there is symmetry of adaptation after increments and decrements of $d \ln g/dt = (1/g)dg/dt = -(1/a)da/dt = -d \ln a/dt$, that is, for the gain (or, equivalently, attenuation) signal plotted on a logarithmic axis. In fact,
a linear function \( f(x) = d - kx \) attains this, as can be immediately proved from equation 5.2. As was seen in section 2.1, a linear function \( f(x) = c - kx \) (or, equivalently, \( h(x) = 1/(c - kx) \) in model \( D_{LN} \)) leads to a Naka-Rushton relation \( O_s(I_s) = cI_s/(1 + kI_s) \) for the steady-state output (Heeger, 1992).

### 5.3 Increment and Decrement Symmetry for Model \( M_{NL} \) Is Obtained When \( h(x) = c \ln(k/x) \), and for Model \( D_{NL} \) When \( h(x) = c \ln(kx) \).

Also for the models \( M_{NL} \) (see Figure 1A) and \( D_{NL} \) (see Figure 1C) in which the nonlinearities in the feedback loops precede the low-pass filtering, choices exist for these nonlinearities such that adaptation immediately after a step input is symmetric for increment versus decrement steps. Contrary to equations 5.1 and 5.2 for models \( D_{LN} \), respectively \( M_{LN} \), that have a differential expression in their right-hand side (which can immediately be solved), symmetry for models \( M_{NL} \) and \( D_{NL} \) leads to functional equations, which can be much harder to solve (Aczel & Dhombres, 1989). In appendix A we show how to derive these functional equations and how to solve them by transforming the functional equations into differential equations. Table 1 includes the results for the functions \( f(x) = c \ln(k/x) \) of model \( M_{NL} \) and \( h(x) = c \ln(kx) \) of model \( D_{NL} \) that yield increment and decrement symmetry of adaptation immediately after the input steps. When plotted on axes such that these resulting functions yield straight lines, the resulting asymmetries of adaptation for other functions \( f \) and \( h \) can be judged by their curvature.

### 6 Dynamics of the Output

So far we have concentrated on the dynamics of the control signals, \( a(t) \) and \( g(t) \), of the models in Figure 1. This is a sensible approach for applications in psychophysics where the control signal \( a(t) \), or \( g(t) \), determines the detectability of a test signal that is superimposed on a background \( I(t) \) (Snippe et al., 2004). Also in a neurophysiological context, control signals such as \( a(t) \) and \( g(t) \) will be important determinants of neural detectability, signal-to-noise ratio, and information transmission. Nevertheless, in physiological experiments, one often directly observes the output signal \( O(t) \) but not the control signal \( a(t) \) or \( g(t) \). Here we study the dynamical behavior of the output \( O(t) \) of the control loops in Figure 1. In particular, we are interested if for monotonic input \( I(t) \), the output \( O(t) \) will also be monotonic, or whether \( O(t) \) can have overshoots or oscillations when \( I(t) \) is monotonic. Obviously, when \( I(t) \) increases very fast (e.g., step-wise), \( O(t) \) will have an overshoot, because the control signals in Figure 1 cannot completely follow these rapid changes in \( I(t) \) due to the low-pass filtering in the feedback loops. Likewise, when \( I(t) \) decreases very fast, \( O(t) \) will have an undershoot. Hence, to obtain simple (monotonic) behavior of \( O(t) \), restrictions on \( dI(t)/dt \) are needed. A reasonable choice to obtain such a restriction is to suppose, as illustrated in Figure 8, that the input \( I(t) \) to the gain control
Table 1: Feedback Nonlinearities Yielding Symmetry.

<table>
<thead>
<tr>
<th>Model</th>
<th>( \frac{dg}{dt} )</th>
<th>( \frac{1}{g} \frac{dg}{dt} )</th>
<th>( \frac{1}{g^2} \frac{dg}{dt} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( M_{NL} )</td>
<td>( c \ln(k/x) )</td>
<td>( c - kx )</td>
<td>( c - kx^2 )</td>
</tr>
<tr>
<td>( M_{LN} )</td>
<td>( \sqrt{c - kx} )</td>
<td>( c - kx )</td>
<td>( (1/c) \exp(-kx) )</td>
</tr>
<tr>
<td>( D_{NL} )</td>
<td>( \frac{da}{dt} )</td>
<td>( \frac{(1/a)da}{dt} )</td>
<td>( \frac{(1/a^2)da}{dt} )</td>
</tr>
<tr>
<td>( D_{LN} )</td>
<td>( c \ln(kk) )</td>
<td>( c - (k/x) )</td>
<td>( c - (k/x^2) )</td>
</tr>
</tbody>
</table>

Notes: Mathematical form of the nonlinearities in the feedback paths of the models in Figure 1 such that adaptation is equally fast (i.e., symmetric) immediately after increment steps \( I_- \rightarrow I_+ \) and decrement steps \( I_+ \rightarrow I_- \) of the input. The second column shows the nonlinearities necessary to obtain increment or decrement symmetry of the gain \( g(t) \) (for models \( M_{NL} \) and \( M_{LN} \)), respectively the attenuation \( a(t) \) (for models \( D_{NL} \) and \( D_{LN} \)). The third column shows the nonlinearities for which one obtains symmetry on a logarithmic scale for the gain, respectively the attenuation. Note that since \( d \ln g/dt = (1/g)dg/dt \) (and similar for \( a(t) \)) this corresponds to the case where the speed of adaptation of \( g \), respectively \( a \), relative to its initial value is symmetric. The fourth column shows the nonlinearities that yield symmetry when the control signal \( g(t) \) in models \( M_{NL} \) and \( M_{LN} \) is plotted as an attenuation \( a(t) = 1/g(t) \), and likewise when \( a(t) \) in models \( D_{NL} \) and \( D_{LN} \) is plotted as a gain \( g(t) = 1/a(t) \). Since \( d(1/g)/dt = -(1/g^2)dg/dt \) (and similar for \( a(t) \)), this corresponds to the case where the speed of adaptation of \( g \), respectively \( a \), relative to the square of its initial value is symmetric. The parameters \( c \) and \( k \) should be chosen positive.

Figure 8: In section 6, the input \( I(t) \) to the gain control (here illustrated for model \( D_{NL} \)) is a low-pass filtered version (time constant \( \tau_I \)) of a signal \( J(t) \) that steps from \( J = J_0 \) to \( J = J_1 \) at time \( t = 0 \).

is a low-pass filtered version of a signal \( J(t) \). Since all neural systems incorporate low-pass filtering, for instance, associated with membrane time constants, this is a reasonable choice. In this section, we assume that \( J(t) \) is a step function \( J_0 \rightarrow J_1 \) at time \( t = 0 \). In fact, it can be shown that when the output \( O(t) \) of the gain control is monotonic for such a step \( J(t) \), it will certainly be monotonic when \( J(t) \) would be a smoother function than a step (i.e., when there would be more low-pass filtering before the gain control). The actual input \( I(t) \) to the gain control loop is assumed to be the result of applying a first-order low-pass filter with time constant \( \tau_I \) to the step
function \( J(t) \), that is, for \( t > 0 \), we assume

\[
\tau_I \frac{dI}{dt} = J_1 - I. \tag{6.1}
\]

The resulting input \( I(t) \) to the gain controls of Figure 1 can be written explicitly as

\[
I(t) = J_1 + (J_0 - J_1) \exp(-t/\tau_I). \tag{6.2}
\]

The question we pose here is, What we can expect for the dynamics of the output \( O(t) \) when the models of Figure 1 are stimulated with the input, equation 6.2? It turns out that the qualitative nature of \( O(t) \) depends critically on the value of the time constant \( \tau_I \) of the filtering of the input in equation 6.1 relative to the time constant \( \tau \) of the low-pass filtering in the feedback controls of Figure 1. In the next section, we study the case where the input steps are small (i.e., \( J_1 - J_0 \ll J_0 \)), in which case the models of Figure 1 can be linearized. In sections 6.2 to 6.4, we study the full nonlinear case.

### 6.1 Linearized Models Have Monotonic Output When \( \tau \leq \tau_I \).

For explicitness we apply linearization to model \( D_{NL} \) (see Figure 1C), but the other three models in Figure 1 can be linearized in the same way, and in fact the linearized forms of the four models in Figure 1 are identical. To apply linearization, we assume

\[
I(t) = [1 + i(t)]I_s, \tag{6.3}
\]
\[
O(t) = [1 + o(t)]O_s, \tag{6.4}
\]
and

\[
a(t) = [1 + \eta(t)]a_s, \tag{6.5}
\]

with \( i(t) \), \( o(t) \), and \( \eta(t) \) all small relative to 1. Note that \( i(t) \), \( o(t) \), and \( \eta(t) \) are dimensionless and will be referred to below as input modulation, output modulation, and control modulation, respectively. The constant steady-state values \( I_s \), \( O_s \), and \( a_s \) are related through \( O_s = I_s/a_s \) and \( a_s = h(O_s) \). The dynamic signals \( i(t) \), \( o(t) \), and \( \eta(t) \) are related through \( 1 + o(t) = (1 + i(t))/(1 + \eta(t)) \). Using the fact that these signals are small relative to 1, \( 1 + o = (1 + i)/(1 + \eta) \approx (1 + i)(1 - \eta) = 1 + i - \eta - i\eta \approx 1 + i - \eta \), and thus

\[
o(t) = i(t) - \eta(t). \tag{6.6}
\]
that is, the linearized system behaves as a subtractive feedback in which
the control modulation \( \eta(t) \) is subtracted from the input modulation \( i(t) \) to
obtain the output modulation \( o(t) \). In appendix B, we prove that when the
input modulation \( i(t) \) is a low-pass filtered step function, as in equation
6.2, the output modulation \( o(t) \) has an overshoot when the time constant
\( \tau \) of the low-pass filter in the control path is larger than the time constant
\( \tau_I \) of the filtering at the input. In this case, the control modulation \( \eta(t) \)
cannot follow the increase in the input modulation \( i(t) \) fast enough, and the
resulting output modulation \( o(t) \) has an overshoot relative to its final steady
state. On the other hand, when \( \tau \leq \tau_I \), the filter in the feedback path is fast
enough to follow the input modulation, and the output modulation \( o(t) \) will
approach its new steady state in a monotonic way, without an overshoot.

6.2 Output of Model \( D_{NL} \) Resembles the Output of the Linearized
Model. As shown in appendix B, when the linearized models are stimu-
lated with low-pass filtered steps, the qualitative dynamics of the output of
these models is quite simple: the sum of a constant and two exponentials.
Depending on the time constants of the low-pass filters, the output is ei-
ther monotonic, or it has a single overshoot (respectively, undershoot for a
decrement step). In this section we show that, remarkably, for model \( D_{NL} \n\) (see Figure 1C), this qualitative dynamics persists also for large input steps,
independent of the precise form of the nonlinearity \( h \) in the feedback path.
For the other models in Figure 1, however, qualitatively new features in the
output can occur, depending on the size and sign of the input steps and on
the form of the nonlinearities in the feedback loops.

When stimulated with an input \( I(t) \), the output \( O(t) \) of model \( D_{NL} \) can
be written as \( O(t) = I(t)/a(t) \). Differentiating this expression with respect
to time yields

\[
\frac{dO}{dt} = \frac{1}{a^2} \left[ a \frac{dI}{dt} - I \frac{da}{dt} \right] = \frac{1}{a^2} \left[ a \frac{J_1 - I}{\tau_I} - I \frac{h(O) - a}{\tau} \right]
\]

\[
= \frac{1}{a} \left[ \frac{J_1 - I}{\tau_I} - \frac{Oh(O) - I}{\tau} \right],
\]  
(6.7)

where we used equations 6.1 and 2.2. Now if \( O(t) \) has an overshoot, \( dO/dt = 0 \) at some finite time \( t \) where the overshoot reaches its maximum value.
Setting \( dO/dt = 0 \) in equation 6.7 yields

\[
Oh(O) = \frac{\tau}{\tau_I} J_1 + \left( 1 - \frac{\tau}{\tau_I} \right) I.
\]  
(6.8)

When plotted in an input-output diagram with the input \( I \) on the horizontal
axis and \( Oh(O) \) on the vertical axis (such that steady-state, \( I_s = O_h(O_s) \), is
a straight line through the origin), equation 6.8 yields for any value of \( \tau/\tau_I \)
Figure 9: (A) Dynamics of the output $O$ of model $D_{NL}$ (with $h(O) = O^2$) stimulated with a low-pass filtered step (time constant $\tau_I$) when $\tau < \tau_I$ ($\tau = 0.5 \tau_I$ in this example). The horizontal axis is the input $I$ from equation 6.2 (with $J_0 = 1$ and $J_1 = 4$). The vertical axis is a nonlinear transformation $Oh(O) = O^3$ of the output of $O$ the model, such that steady state $O^3_s = I_s$ (dotted line) is a straight line through the origin. According to equation 6.8, the line $dO/dt = 0$ (dashed line) also is a straight line in these coordinates, with positive slope when $\tau < \tau_I$. Hence, the actual (nonlinearly transformed) output $O^3(I)$ (continuous line) cannot cross this line and must remain in the region below the dashed line, where $dO/dt > 0$, hence $O(t)$ is monotonic. (B) As A, but now with $\tau = 2 \tau_I$, such that equation 6.8, $dO/dt = 0$ (dashed line), has negative slope and therefore can be crossed by the actual output $O^3(I)$ (continuous curve labeled “large step”). In fact, a crossing always occurs since the output cannot cross the output of the linearized model valid for small steps (continuous curve labeled “small step”), which has an overshoot when $\tau > \tau_I$, as derived in appendix B. Thus, $O(t)$ has a single overshoot, and it has a single undershoot (not shown in the figure) after a decrement step in the input.

A straight line (see Figure 9). This line separates the region above the line where $dO/dt < 0$ from the region below it where $dO/dt > 0$. Note that the line where $dO/dt = 0$ (given by equation 6.8) crosses the steady-state line, $I_s = Oh(O_s)$, when $I = J_1$. Now consider the case that $\tau / \tau_I < 1$: thus, the low-pass filter in the feedback control is faster than the filtering at the input. Then the line given by equation 6.8 has a positive slope $1 - \tau / \tau_I$ (smaller than 1), as illustrated in Figure 9A. When the step $J_0 \rightarrow J_1$ at $t = 0$ is an increment (i.e., when $J_0 < J_1$), the system will start at $t = 0$ from a point $I = Oh(O) = J_0 < J_1$ on the steady-state line, and according to equation 6.7, $dO/dt > 0$. Thus, for $t > 0$ the output $O(t)$ initially increases. And in fact it will continue to increase (toward its final steady-state level where $Oh(O) = I = J_1$) for all $t > 0$. This is because the output $O(t)$ cannot cross the line where $dO/dt = 0$, since on this line, $dO/dt = 0$, but for $I < J_1$, according to equation 6.1, $dI/dt > 0$. Hence, if $O(t)$ approaches the line $dO/dt = 0$, it will be pushed back in the region where $dO/dt > 0$. Thus, when $\tau < \tau_I$, $O(t)$
approaches its final steady state in a monotonic way, without an overshoot (illustrated in Figure 9A for the case \( h(O) = O^2 \)). Likewise, when the step \( J_0 \rightarrow J_1 \) at the input is a decrement step (i.e., when \( J_0 < J_1 \)), the output \( O(t) \) will decrease monotonically and reach its final steady state without an undershoot.

The situation is very different, however, when \( \tau/\tau_I > 1 \)—when the low-pass filter in the feedback loop is slower than the filtering at the input. In that case, the straight line of equation 6.8 has a negative slope, and now the output \( O(t) \) can cross the line \( dO/dt = 0 \), because now if \( O(t) \) approaches the line \( dO/dt = 0 \), it will be pulled into the region with \( dO/dt < 0 \) (see Figure 9B). In fact, from the small-signal analysis performed in appendix B, it follows that such a crossing must occur. In appendix B we showed that when \( \tau/\tau_I > 1 \), for small steps at the input, the resulting output attains its final steady state with an overshoot (the curve labeled “small step” in Figure 9B). But the output for a large step (the curve labeled “large step” in Figure 9B) cannot cross the output for the small step (since both outputs are described by the same first-order differential equation 6.7, implying that their trajectories must be identical if they have a point in common). The result, as illustrated in Figure 9B, is that for a large step, \( O(t) \) will have exactly one overshoot before it reaches steady state for \( t \rightarrow \infty \). Likewise, for a decrement step (i.e., when \( 0 < J_1 < J_0 \) in equation 6.2), \( O(t) \) will have exactly one undershoot (without any subsequent overshoot) when \( \tau/\tau_I > 1 \). Thus, remarkably, the qualitative dynamics of the output \( O(t) \) of the nonlinear divisive model \( D_{NL} \) is identical to the behavior of its linearized version analyzed in appendix B.

### 6.3 The Output of Model \( M_{NL} \) Can Have Overshoots Also When \( \tau < \tau_I \)

The qualitative dynamics of the output \( O(t) \) of the multiplicative model \( M_{NL} \) (see Figure 1A), however, can differ from the linear analysis of appendix B. When stimulated with input \( I(t) \), this model yields an output \( O(t) = I(t)g(t) \), hence using equations 6.1 and 2.1,

\[
\frac{dO}{dt} = g \frac{dI}{dt} + I \frac{dg}{dt} = g \left( \frac{J_1 - I}{\tau_I} + I \frac{f(O) - g}{\tau} \right) = g \left[ \frac{J_1 - I}{\tau_I} - \frac{I - I^2 f(O)/O}{\tau} \right].
\]  

(6.9)

Setting \( dO/dt = 0 \) in equation 6.9 yields

\[
\frac{O}{f(O)} = \frac{I^2}{I (\tau/\tau_I + 1) - J_1 \tau/\tau_I},
\]  

(6.10)

which, contrary to the corresponding equation 6.8 for model \( D_{NL} \), is a non-linear equation in \( I \). The behavior of equation 6.10 is illustrated for a number
of values of $\tau/\tau_I$ by the dashed curves in Figure 10. When $\tau > \tau_I$, that is, when the filter in the feedback loop is slower than the filtering of the input, the structure of the lines in Figure 10 is such that the qualitative behavior of $O(t)$ is identical to the behavior for $\tau > \tau_I$ of the output of model $D_{NL}$. After an increment step at the input, $O(t)$ has a single overshoot, and after a decrement step, $O(t)$ has a single undershoot. For an increment step, this result follows using the reasoning for model $D_{NL}$ in Figure 9B, since in both Figure 9B and Figure 10, the lines $dO/dt = 0$ are monotonically decreasing when $I < J_1$ and $\tau > \tau_I$. For $I > J_1$ the lines $dO/dt = 0$ are nonmonotonic when $\tau > \tau_I$; they have a minimum at a finite value of $I$ and then increase with increasing $I$. However, this does not affect the qualitative behavior of $O(t)$ since $O(t)$ cannot cross this increasing part of the curve $dO/dt = 0$. Thus, when $\tau > \tau_I$ the output $O(t)$ has a single undershoot after a decrement step at the input. Now consider the case that $\tau < \tau_I$—the case that the filter in the feedback path is faster than the filter at the input. After a decrement step of the input, the output $O(t)$ is qualitatively identical to the output of model $D_{NL}$ and will reach steady state without an undershoot. This follows from the fact that the curves $dO/dt = 0$ in Figure 10 are monotonically increasing when $I > J_1$ and $\tau < \tau_I$; hence, the qualitative dynamics for $O(t)$ in this case is identical to that obtained for model $D_{NL}$. After an increment step, however, now $O(t)$ can be qualitatively different from the output of
model $D_{NL}$, because the curves $dO/dt = 0$ in Figure 10 now have a more complicated structure than in Figure 9A, with a sharp upturn for small values of $I$. As a consequence, whereas model $D_{NL}$ reaches steady state in a monotonic fashion when $\tau < \tau_I$, the output $O(t)$ of model $M_{NL}$ develops a “nose” for sufficiently large steps at the input. That is, after large steps of the input $I(t)$, the output $O(t)$ of model $M_{NL}$ has an initial overshoot, followed by a subsequent undershoot, as shown by the continuous curve in Figure 10.

### 6.4 Simple Input Can Yield a Complicated Output in Models $D_{LN}$ and $M_{LN}$

Model $D_{LN}$ (or, equivalently, model $M_{LN}$) can have an output $O(t)$ that is still more complicated than the output of model $M_{NL}$ shown in Figure 10. When the nonlinearity $h(x)$ (though monotonic) has sign changes in its second-order derivative $d^2h/dx^2$, the output $O(t)$ of model $D_{LN}$ can have oscillatory features when the model is stimulated with the simple low-pass filtered step of equation 6.2. An example is shown in Figure 11.

### 7 Discussion

In this letter, we studied the dynamics of the four feedback models for gain control shown in Figure 1. Two of the models ($M_{NL}$ and $M_{LN}$) have a multiplicative gain control, whereas the other two models ($D_{NL}$ and $D_{LN}$) have a divisive gain control. The structure of all four models is very similar in that the feedback loop for each consists of a concatenation of an instantaneous nonlinearity and a first-order low-pass filter. As shown
in sections 2.2 and 2.3, two of these models ($M_{LN}$ and $D_{LN}$) are actually identical, and the other two models ($M_{NL}$ and $D_{NL}$) are connected by a duality. Despite these relationships, however, the dynamics of models $M_{NL}$, $D_{NL}$, and $M_{LN}$ (c.q. $D_{LN}$) can be very different for a given input $I(t)$. For instance, in section 4, we showed that the dynamics of adaptation of the models differs after steps in the input (see Figures 5 and 7), and in section 5 we showed that the models differ in their asymmetries of adaptation after increments and decrements of the input. Finally, in section 6, we showed that for simple band-limited inputs $I(t)$, the outputs $O(t)$ of the different models can be qualitatively different. Thus, subtle differences in the control structure of feedback models for gain control can have strong effects on their dynamics.

As shown in section 6, the input-output behavior of model $D_{NL}$ is qualitatively the simplest, especially when $\tau < \tau_I$ (see Figure 9A), because in that case, a monotonic input $I(t)$ yields a monotonic output $O(t)$. Thus, when a nonmonotonic output $O(t)$ occurs in model $D_{NL}$, the corresponding input $I(t)$ also must have been nonmonotonic. On the other hand, even when $\tau < \tau_I$, model $M_{NL}$ can have a nonmonotonic output $O(t)$ when the input $I(t)$ was monotonic, as is shown in Figure 10. Finally, model $D_{LN}$ (and model $M_{LN}$) can give complicated outputs even when the input is simple. Hence, for this model, it can be difficult to make a qualitative estimate of the input when observing the output. For instance, it would be hard to discriminate the output seen for this model in Figure 11 from an output generated by this model when stimulated by an input that genuinely oscillates. It appears therefore that model $D_{NL}$ is usually a safer design than the models $M_{NL}$ and (especially) $M_{LN}$ or $D_{LN}$, since as a general principle in information processing, one should try to avoid introducing spurious structure that is not present at the input (Koenderink, 1984).

The structural complexity of the models studied in this letter has been kept to a minimum. The great advantage of this approach is that we can obtain general results using an exact mathematical analysis. It would be very hard to derive conclusions of similar generality if one would have to resort to numerical simulations, which might be necessary for more complex models. Nonetheless, the results derived for the simple models studied here can aid in the analysis of more complex models. For instance, the results derived here can speed the search for realistic complex models by restricting the huge search space of the many possible complex models to more manageable proportions. A realistic strategy for this would be to first investigate the steady-state behavior of the system under study, which determines the mathematical form of the nonlinearity in the system (Chichilnisky, 2001; Snippe et al., 2004). Given the steady state, one can then study the dynamics of the system (e.g., increment and decrement asymmetry and overshoots of the output) to determine which type of model (e.g., divisive or multiplicative) is appropriate to explain the experimental data.
Figure 12: An example of nonlinear (divisive) control (A) where the nonlinearity and the filtering shape not only the control signal $a(t)$ but also directly the output $O(t)$. The model is equivalent to the model shown at the right (B). Hence, the dynamics of $a(t) = O(t)$ of this model can be studied with the methods developed for model $D_{NL}$ in Figure 1.

There are several simple extensions and alternatives of the models studied here that are amenable to analysis with the methods developed here. For instance, the filtering and nonlinearities in the feedback path in Figure 1 could also be placed at a point before the feedback loop branches off from the output. As shown in Figure 12, this in fact does not affect the dynamics of the gain signal, but it changes the dynamics of the output, which now becomes identical to the gain. Finally, the filtering operations could be generalized. For instance, one could consider higher-order low-pass filters, time delays in the filters, or high-pass filtering of the output (Berry et al., 1999). It is well known that with increasing values of the input (e.g., luminance or contrast), neural systems not only decrease their gain but also adapt their temporal filtering (e.g., Sperling & Sondhi, 1968; Victor, 1987; Benardete, Kaplan, & Knight (1992); Carandini & Heeger, 1994; van Hateren, 2005). It will be interesting to see to what extent the tools developed in this letter can also be used to analyze such more general systems.

Appendix A: Increment and Decrement Symmetry for Models $D_{NL}$ and $M_{NL}$

Adaptation in model $D_{NL}$ (see Figure 1C) is described by

$$\tau \frac{da}{dt} = h(O) - a = h\left(\frac{I}{a}\right) - a.$$  \hspace{1cm} (A.1)

For a constant input $I_s$, steady state is attained when $da/dt = 0$, thus, when $h(1/a_s) = a_s$. Hence, in steady state $I_s = a_s h^{-1}(a_s) = O_s h(O_s)$, where $h^{-1}$ is the inverse of the function $h$, and we have used the fact that in steady state $a_s = h(O_s)$. Now consider an increment step $I_- \rightarrow I_+$ of the input. For the input $I_-$ the steady-state equation is $I_+ = a_- h^{-1}(a_-) = O_- h(O_-)$, and for the input $I_+$ it is $I_+ = a_+ h^{-1}(a_+) = O_+ h(O_+)$. Immediately after the increment step, when the input is $I_+$ but the attenuation $a$ is still at its old
adaptation level $a_-$,
\[
\tau \frac{da_{\text{inc}}}{dt} = h \left( \frac{I_+}{a_-} \right) - a_- = h \left( \frac{I_+}{a_-} \right) - h \left( \frac{I_-}{a_-} \right) = h \left( \frac{O_+ h (O_+)}{h (O_-)} \right) - h (O_-).
\] (A.2)

Likewise, immediately after a decrement step $I_+ \to I_-$,
\[
\tau \frac{da_{\text{dec}}}{dt} = h \left( \frac{O_- h (O_-)}{h (O_+)} \right) - h (O_-).
\] (A.3)

For symmetry of adaptation, we equate $\frac{da_{\text{inc}}}{dt}$ and $-\frac{da_{\text{dec}}}{dt}$ (taking into account that $a$ decreases after a decrement step). Writing $O_+ = y$ and $O_- = x$, this yields
\[
h \left( \frac{yh (y)}{h (x)} \right) + h \left( \frac{xh (x)}{h (y)} \right) = h (y) + h (x),
\] (A.4)
a functional equation for $h$ in terms of two variables $x$ and $y$ (Aczel & Dhombres, 1989). It is easy to verify that equation A.4 is solved by the function $h(x) = c + k \ln x$ (with $c$ and $k$ constants; $k > 0$ for gain control), but how does one obtain such a solution? A method to solve A.4 is to set $y = x + \epsilon$ and make a Taylor expansion of the resulting expression. Since, as shown below, terms up to the first order in the expansion cancel, it is necessary to expand to second order in $\epsilon$. An identical result can be obtained by differentiating equation A.4 twice with respect to $y$, and putting $y = x$ after differentiating. Taylor-expanding the right-hand side of equation A.4 yields
\[
h (x + \epsilon) + h (x) = 2h (x) + \epsilon \frac{dh (x)}{dx} + \frac{1}{2} \epsilon^2 \frac{d^2 h (x)}{dx^2} = 2h + \epsilon h' + \frac{1}{2} \epsilon^2 h'',
\] (A.5)
where for conciseness, we write $dh/dx = h'$ and $d^2 h/dx^2 = h''$, and drop the argument $x$ everywhere. Likewise, the left-hand side of equation A.4 yields
\[
h \left( \frac{(x + \epsilon) (h + \epsilon h' + \epsilon^2 h''/2)}{h} \right) + h \left( \frac{xh}{h + \epsilon h' + \epsilon^2 h''/2} \right)
\]
\[
= h \left( (x + \epsilon) \left( 1 + \epsilon \frac{h'}{h} + \frac{\epsilon^2 h''}{2h} \right) \right) + h \left( \frac{x}{1 + \epsilon h'/h + \epsilon^2 h''/2h} \right).
\]
\[ h(x + \varepsilon \left[ 1 + \frac{x h'}{h} \right] + \varepsilon^2 \left[ \frac{h'}{h} + \frac{x h''}{2h} \right]) + \varepsilon \left( x - \frac{x h'}{h} - \varepsilon^2 \left[ \frac{x h''}{2h} - x \left( \frac{h'}{h} \right)^2 \right] \right) \]

\[ = h + \varepsilon \left[ 1 + \frac{x h'}{h} \right] h' + \varepsilon^2 \left[ \frac{h'}{h} + \frac{x h''}{2h} \right] h' + \frac{\varepsilon^2}{2} \left[ 1 + \frac{x h'}{h} \right]^2 h'' \]

\[ + \varepsilon \left( x - \frac{x h'}{h} - \varepsilon^2 \left[ \frac{x h''}{2h} - x \left( \frac{h'}{h} \right)^2 \right] \right) h' + \frac{\varepsilon^2}{2} \left( \frac{x h'}{h} \right)^2 h'' \]

\[ = 2h + \varepsilon h' + \varepsilon^2 \left\{ \left( \frac{h'}{h} \right)^2 + \frac{h''}{2} \left[ 1 + \frac{x h'}{h} \right]^2 + x h' \left( \frac{h'}{h} \right)^2 + \frac{h''}{2} \left( \frac{x h'}{h} \right)^2 \right\}. \] (A.6)

Equating A.6 and A.5, only terms in \( \varepsilon^2 \) remain:

\[ \varepsilon^2 \left\{ \left( \frac{h'}{h} \right)^2 + \frac{1}{2} h'' + \frac{x h' h''}{h} + \left( \frac{x h'}{h} \right)^2 h'' + x \left( \frac{h'}{h} \right)^3 \right\} = \frac{1}{2} \varepsilon^2 h''. \] (A.7)

Cancelling the right-hand side of equation A.7 with the second term on the left-hand side of equation A.7, and multiplying with \( h^2 / \varepsilon^2 h' \) yields

\[ h h' + x h h'' + x^2 h' h'' + x \left( h' \right)^2 = 0, \] (A.8)

which can be simplified to

\[ [h + x h'] \cdot [h' + x h''] = [xh]' \cdot [xh'] = 0. \] (A.9)

The first factor in equation A.9, \([xh]' = 0\), has a solution \( h(x) = k/x \) that decreases with increasing \( x \), contrary to the assumptions in section 2. However, the second factor in equation A.9, \([xh]' = 0\), does yield a result for divisive gain control. Because \([xh]' = 0\) means \( xh' = c \) with \( c \) a constant (positive for divisive gain control), it follows that \( h' = c/x \), thus \( h(x) = c \ln(kx) \), with \( k \) another positive constant. Note that when \( x < 1/k \), \( h(x) = c \ln(kx) \) becomes negative, which speeds up adaptation after large decrements of the input. However, in steady state, \( I_s = O_s f(O_s) = O_s c \ln(kO_s) > 0 \), hence \( h(O_s) = c \ln(kO_s) > 0 \).

The method used here to derive a functional equation and transform it into a differential equation can also be used to find nonlinearities \( f(x) \) that yield symmetric adaptation immediately after increment and decrement steps of the input in the multiplicative model \( M_{NL} \). Likewise,
nonlinearities can be found for which \((1/a)da/dt = d\ln a/dt\) (or, equivalently, \((1/g)dg/dt = d\ln g/dt\)) is symmetric immediately after increment and decrement steps. Results are collected in Table 1.

**Appendix B: Dynamics of the Output for the Linearized Models**

To obtain an explicit expression for the output modulation \(o(t)\) (see equation 6.6), we linearize the dynamics of the feedback loop of model \(D_{NL}\), equation 2.2, which yields

\[
\tau \frac{da(t)}{dt} = h(O(t)) - a(t) = h(O_s) + O_s h'(O_s) o(t) - a_s - a_s \eta(t) = O_s h'(O_s) o(t) - h(O_s) \eta(t).
\]  \(\text{(B.1)}\)

In the first step of equation B.1, we used the steady-state relation \(a_s = h(O_s)\), and defined \(h'(O_s) = dh(O_s)/dO_s\). Using equation 6.5 and the steady-state relation \(a_s = h(O_s)\), the left-hand side of equation B.1 can be rewritten as \(\tau h(O_s) \eta(t)/dt\). Using equation 6.6, we can rewrite equation B.1 as

\[
\tau \frac{d\eta(t)}{dt} = Qi(t) - (1 + Q) \eta(t),
\]  \(\text{(B.2)}\)

where we define

\[
Q \equiv O_s h'(O_s)/h(O_s).
\]  \(\text{(B.3)}\)

Note that in general, the parameter \(Q\) in equation B.3 depends on the steady-state output \(O_s\), \(Q = Q(O_s)\). For conciseness, we have suppressed this dependence in our notation. Dividing equation B.2 by \(1 + Q\) yields

\[
\tau_Q \frac{d\eta(t)}{dt} = \frac{Q}{1 + Q} i(t) - \eta(t),
\]  \(\text{(B.4)}\)

where we defined \(\tau_Q = \tau/(1 + Q)\). Equation B.4 says that for the linearized model, the subtractive control modulation \(\eta(t)\) is a low-pass filtered version of the input modulation \(i(t)\), in which the filter has a gain \(Q/(1 + Q)\) and a time constant \(\tau_Q = \tau/(1 + Q)\) (Bechhoefer, 2005). Equation B.4 can be solved explicitly when the input modulation \(i(t)\) is a low-pass filtered step of size \(s\), that is, when for \(t \geq 0\),

\[
i(t) = s[1 - \exp(-t/\tau_I)],
\]  \(\text{(B.5)}\)

and for \(t < 0\), \(i(t) = 0\). The solution of the linear equation B.4 (representing a first-order low-pass filter) can be written as the convolution of \(i(t)\) with a
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low-pass filter with time constant $\tau_Q$ and gain $Q/(1 + Q)$:

$$\eta(t) = \frac{Q}{(1 + Q)\tau_Q} \int_0^t i(t') \exp\left(-\frac{t - t'}{\tau_Q}\right) dt',$$

(B.6)

where the fact that $i(t') = 0$ for $t' < 0$ has been used for the lower bound of the integral. Substituting equation B.5 into equation B.6, the integral is elementary and yields

$$\eta(t) = \frac{s Q}{1 + Q} \left\{ 1 + \frac{\tau_Q}{\tau_I - \tau_Q} \exp\left(-\frac{t}{\tau_Q}\right) \right. $$

$$- \left. \frac{\tau_I}{\tau_I - \tau_Q} \exp\left(-\frac{t}{\tau_I}\right) \right\} \quad \text{when} \quad \tau_I \neq \tau_Q, \quad \text{(B.7)}$$

and

$$\eta(t) = \frac{s Q}{1 + Q} \left\{ 1 - \left( 1 + \frac{t}{\tau_Q} \right) \exp\left(-\frac{t}{\tau_Q}\right) \right\} \quad \text{when} \quad \tau_I = \tau_Q. \quad \text{(B.8)}$$

First, we study the case $\tau_I \neq \tau_Q$. For this case, using equations 6.6, B.5, and B.7, the output modulation $o(t)$ of the gain control is

$$o(t) = i(t) - \eta(t) = \frac{s}{1 + Q} - \frac{s (\tau_I - \tau)}{(1 + Q) (\tau_I - \tau_Q)} \exp\left(-\frac{t}{\tau_I}\right) $$

$$- \frac{s Q \tau_Q}{(1 + Q) (\tau_I - \tau_Q)} \exp\left(-\frac{t}{\tau_Q}\right), \quad \text{(B.9)}$$

where in the second term of equation B.9, we used the relation $\tau = (1 + Q)\tau_Q$. Now when $\tau < \tau_I$ (i.e. when the low-pass filter in the control loop is faster than the filter at the input), the prefactors of the exponential functions in equation B.9 are both positive, and hence $o(t)$ is a monotonically increasing function. Thus, when $\tau < \tau_I$, the output modulation $o(t)$ reaches its final value $s Q/(1 + Q)$ in a monotonic way, without any overshoots or oscillations.

When $\tau > \tau_I$ (i.e., when the low-pass filter in the control loop is slower than the filter at the input), two situations can occur, depending on the value of the parameter $Q$ in equation B.3: either $\tau_Q = \tau/(1 + Q) < \tau_I$, or $\tau_Q > \tau_I$. If $\tau_Q > \tau_I$, then at large times $t$, the exponential function $\exp\left(-t/\tau_Q\right)$ in equation B.9 will dominate the exponential function $\exp\left(-t/\tau_I\right)$. However, $\tau_Q > \tau_I$ means that $\tau_I - \tau_Q < 0$; hence, in this case, the contribution of $\exp\left(-t/\tau_Q\right)$ to the result B.9 will be positive, which means that for large $t$, the output modulation $o(t)$ in equation B.9 approaches its final value $s Q/(1 + Q)$ from above. This, however, can be the case only when $o(t)$ has
an overshoot. Likewise, when $\tau_Q < \tau_I$, the exponential $\exp(-t/\tau_I)$ dominates $\exp(-t/\tau_Q)$ for large $t$. However, in this case, the contribution of $\exp(-t/\tau_I)$ to $\eta(t)$ is positive, as can be easily verified. Hence, when $\tau > \tau_I$, the output modulation $\eta(t)$ always has an overshoot, independent of the precise value of $\tau_Q$ relative to $\tau_I$. One can easily check that $\eta(t)$ also has a single overshoot when $\eta(t)$ is described by equation B.8, that is, when $\tau_I = \tau_Q$ exactly (and hence $\tau = (1 + Q)\tau_Q > \tau_I$).

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References


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