

## Adaptation and gain normalization: a comment on Ullman & Schechtman (1982)

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A well-known process for adaptation and gain normalization is compared with the process described by S. Ullman and G. Schechtman (*Proc. R. Soc. Lond. B* **216**, 299–313 (1982)). A neural interpretation of this process in terms of transmitter gating, slow accumulation, and release is described. Applications to a wide variety of problems in perception, cognition, and motivated behaviour can be made by embedding the gating process into opponent processes, notably shunting on-centre off-surround networks, to form a network module called a gated dipole field.

The article by Ullman & Schechtman (1982) claims to introduce a new mechanism of gain control for perceptual adaptation and normalization. This note shows that the mechanism is not new. It has been used to explain adaptation and normalization effects in a wide variety of perceptual, cognitive, and learning data (Carpenter & Grossberg 1981; Grossberg 1972*a, b*, 1974, 1975, 1976, 1978, 1980*a, b*, 1981*a, b*) since its introduction in the 1960s (Grossberg 1968, 1969).

Ullman & Schechtman (1982) define a process whereby an input  $x$  and an output  $y$  are related by an equation

$$y = gx. \quad (1)$$

In (1),  $g$  is a gain control process that seeks a level

$$k/\bar{x}, \quad (2)$$

where  $k$  is a positive constant and  $\bar{x}$  is the average value of the input  $x$ . They define the process  $g$  iteratively by the rule

$$g_{n+1} = g_n + \delta(k - g_n x_n), \quad (3)$$

where  $\delta$  is a positive constant. This formulation of the problem exhibits a physical anomaly. If the average  $\bar{x}$  approaches zero, then the gain approaches the unphysical value of infinity. If (2) is generalized to

$$k/(\alpha + \bar{x}), \quad (4)$$

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where  $\alpha$  is a non-negative constant, then this problem is avoided by choosing  $\alpha$  to be positive. Correspondingly, the iteration (3) is generalized to

$$g_{n+1} = g_n + \delta[k - g_n(\alpha + x_n)]. \quad (5)$$

When (5) is rewritten as

$$g_{n+1} - g_n = \delta[k - g_n(\alpha + x_n)] \quad (6)$$

and then converted into a differential equation, we find the total process

$$y = gx \quad (1)$$

and

$$dg/dt = \delta[k - g(\alpha + x)]. \quad (7)$$

This process is usually described using a slightly different notation:

$$T = Sz \quad (8)$$

and

$$dz/dt = A(B - z) - CSz. \quad (9)$$

In this notation, the process is interpreted as follows. An input signal  $S$  generates an output signal  $T$  by being *gated* by the process  $z$ . The process  $z(t)$  is physically interpreted as a chemical transmitter that is released via a mass action interaction with  $S$  at a rate proportional to  $T$ . Term  $A(B - z)$  in (9) says that transmitter  $z$  accumulates at a slow rate  $A$  to the maximal value  $B$ . Term  $-CSz$  in (9) says that transmitter is released at rate  $-CSz$  because of a mass action interaction with the input  $S$ . The slow reaction rate of  $z$  determines its ability to average prior levels of  $S$ .

Perceptual applications of this gating process include explanations and predictions about spatial frequency adaptation, monocular and binocular rivalry, switching between ambiguous figures, colour-contingent after effects, intracellular adaptation, Weber law modulation, and habituation (Grossberg 1976, 1980*a*). In order to develop these applications, the chemical gating process was joined to shunting on-centre off-surround networks to form a module called a *gated dipole field*. An example of such a field in colour theory is a network built up from double opponent receptive fields. The transmitter interpretation of the gating process, which is not apparent in the Ullman & Schechtman (1982) treatment, has enabled the theory to explain and predict a variety of physiological data. For example, in applications to visual cortex, the gating process is interpreted as a formal analogue of the noradrenaline arousal system (Grossberg 1972*b*, 1976, 1980*a*). In a model of transduction by a vertebrate cone, the gating process is interpreted as a formal analogue of an intracellular release of  $Ca^{2+}$  (Carpenter & Grossberg 1981). Many other uses of the gating idea have also been made, such as in explanations of how external reinforcements and internal drives are processed by midbrain gated dipole circuits to generate the incentive motivational signals that energize consummatory behaviour (Grossberg, 1972*a, b*, 1975, 1981*b*), and how matching and resetting processes regulate the stable development of perceptual and cognitive codes (Grossberg 1976, 1978, 1980*a*, 1981*a*). These applications go far beyond the results that Ullman & Schechtman (1982) describe in their article.

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