

# How Reliable is the Pattern Adaptation Technique? A Modeling Study

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**Hegd  J.** How reliable is the pattern adaptation technique? A modeling study. *J Neurophysiol* 102: 2245–2252, 2009. First published June 24, 2009; doi:10.1152/jn.00216.2009. Upon prolonged viewing of a sinusoidal grating, the visual system is selectively desensitized to the spatial frequency of the grating, while the sensitivity to other spatial frequencies remains largely unaffected. This technique, known as pattern adaptation, has been so central to the psychophysical study of the mechanisms of spatial vision that it is sometimes referred to as the “psychologist’s microelectrode.” While this approach implicitly assumes that the adaptation behavior of the system is diagnostic of the corresponding underlying neural mechanisms, this assumption has never been explicitly tested. We tested this assumption using adaptation bandwidth, or the range of spatial frequencies affected by adaptation, as a representative measure of adaptation. We constructed an intentionally simple neuronal ensemble model of spatial frequency processing and examined the extent to which the adaptation bandwidth at the system level reflected the bandwidth at the neuronal level. We find that the adaptation bandwidth could vary widely even when all spatial frequency tuning parameters were held constant. Conversely, different spatial frequency tuning parameters were able to elicit similar adaptation bandwidths from the neuronal ensemble. Thus, the tuning properties of the underlying units did not reliably reflect the adaptation bandwidth at the system level, and vice versa. Furthermore, depending on the noisiness of adaptation at the neural level, the same neuronal ensemble was able to produce selective or nonselective adaptation at the system level, indicating that a lack of selective adaptation at the system level cannot be taken to mean a lack of tuned mechanisms at the neural level. Together, our results indicate that pattern adaptation cannot be used to reliably estimate the tuning properties of the underlying units, and imply, more generally, that pattern adaptation is not a reliable tool for studying the neural mechanisms of pattern analysis.

## INTRODUCTION

In a pioneering psychophysical study, Blakemore and Campbell (1969) showed that upon prolonged viewing of a sinusoidal grating, the visual system is selectively desensitized, or adapted, to the spatial frequency of the grating, while the sensitivity to other spatial frequencies remains largely unaffected. They interpreted this as evidence that the visual system processes spatial frequency through mutually independent pathways or “channels.”

Since that time, this technique, referred to variously as selective adaptation, pattern adaptation, pattern-selective adaptation, or contrast adaptation, has become an influential and established technique in psychophysical study of pattern analysis (for reviews, see Braddick et al. 1978; De Valois and De Valois 1988; Graham 1989; Wandell 1995). Indeed the importance of this technique to psychophysics is such that it is

sometimes referred to as the “psychologist’s microelectrode” (Frisby 1979; also see Leopold et al. 2001). Pattern adaptation has been widely used, in one form or another, to study the mechanisms that underlie the processing of spatial frequency or other visual or nonvisual sensory features (for reviews, see Graham 1989; Hollins and Bensma a 2007; Marks 1974; Wark et al. 2007). A closely related technique, functional magnetic resonance imaging adaptation (fMRIa), has also gained much currency (see Grill-Spector and Malach 2001; but see Krekelberg et al. 2006).

The empirical fact that the visual system can and does adapt to visual stimuli is indisputable. So is the experimental utility of the adaptation process as a potentially powerful tool for manipulating the underlying neural mechanisms. But what precisely does adaptation at the system level reveal about the properties of the underlying neural mechanisms? While the key operating assumptions vary considerably from one study to the next, it is fair to say that to a first approximation, the pattern-adaptation technique implicitly assumes that the adaptation parameters at the system level reflect the properties of the underlying units (for overviews, see Graham 1989; Klein 1992; Wandell 1995). That is, previous studies that have used the pattern adaptation technique have generally used some measure of adaptation at the system level (typically adaptation bandwidth) to estimate the corresponding property of underlying neural substrates.

To be sure, many previous studies, including Blakemore and Campbell (1969), have explicitly stated the underlying assumptions of pattern adaptation and have interpreted the results carefully with the applicable caveats in mind (see Graham 1989 for a comprehensive listing of the assumptions). But in the present context, the problem with pattern adaptation is not that its underlying assumptions have been unstated, but that they have gone untested. No study to our knowledge has systematically tested, much less directly established, how adaptation at the neural level relates to the adaptation at the system level, or vice versa (see Krekelberg et al. 2006). Of course, this is not to say that adaptation itself has not been studied at either level. Indeed much is known about the effects of adaptation at both the system and neural levels (for overviews, see Clifford et al. 2007; Graham 1989; Kohn 2007; Krekelberg et al. 2006). But no previous study to our knowledge has directly examined whether or to what extent the adaptation parameters at the neural level can be reliably estimated from the adaptation parameters at the system level.

On the one hand, the proposition of estimating the value of an independent variable (e.g., adaptation bandwidth at the neural level) given the observed value of a potentially multivariate dependent variable (i.e., adaptation bandwidth at the system level) would seem *prima facie* suspect on purely math-

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emational grounds alone. On the other hand, even if adaptation bandwidth at the system level is not a precise estimator of the underlying neural properties, it may nonetheless be useful as a broad, albeit “leaky” measure of the neural properties. Therefore it may be unwise to discount the usefulness of pattern adaptation based on the aforementioned first principles alone. Thus what is needed is an investigation of the relative strengths and weaknesses of using adaptation at the system level as a “marker” for the underlying neural properties.

We therefore investigated the relationship between the adaptation behavior of the system and of the units using modeling. We studied whether and to what extent the adaptation bandwidth at the system level reflects the adaptation bandwidth at the neural level (and vice versa). We focused on adaptation bandwidth because it is a reasonably representative measure of adaptation and has been used in a large number of previous studies and as such is well-suited as a test-case measure for investigating the relationship between adaptation at the system versus neural levels (see Graham 1989; also see following text).

We constructed a simple, biologically plausible, neuronal ensemble model (i.e., population model) that simulated key features of human spatial frequency adaptation, and studied the parameters that affected its adaptation behavior, specifically the adaptation bandwidth. The model was intended to provide a simple, easy-to-understand demonstration of this relationship (or lack thereof) and not necessarily to provide a detailed simulation of spatial frequency processing.

Our results indicate that adaptation behavior of the system is a notably poor measure of the underlying neural mechanisms

of spatial frequency processing. Even more surprisingly, the behavior of the system was often a *misleading* measure of the underlying neural properties.

## METHODS

The construction and testing of the model is described in detail in RESULTS (also see Fig. 1). Briefly, we constructed a simple, single-layered, distributed neuronal ensemble that processed spatial frequency. Except where stated otherwise, the ensemble consisted of 40 units. We determined the contrast sensitivity function (CSF) of the ensemble before and after adaptation. For the adapted ensemble, we also determined the adaptation bandwidth (see following text).

### Determining the CSF of the ensemble

We calculated the response of each unit  $i$  to the test stimulus at spatial frequency  $s$  and at contrast  $c$

$$R_{i,s,c} = h_i(s, c) \quad (i)$$

where  $h_{i,s,c}$  is the joint spatial frequency and contrast tuning curve of the unit.

The variance of the response (i.e., noise) was arbitrarily taken to be

$$\sigma_{i,s,c}^2 = 1.5 R_{i,s,c} \quad (ii)$$

as described previously by Lehky and Sejnowski (1990a, 1999).

We then calculated the response and response variance of each unit of the ensemble at successively higher contrasts ( $c \geq 0$ ) and calculated, for each contrast, the probability  $p$  that the aggregate response (i.e., population response) of the ensemble exceeded the aggregate response to the same stimulus at  $c = 0$  (i.e., equiluminance) using

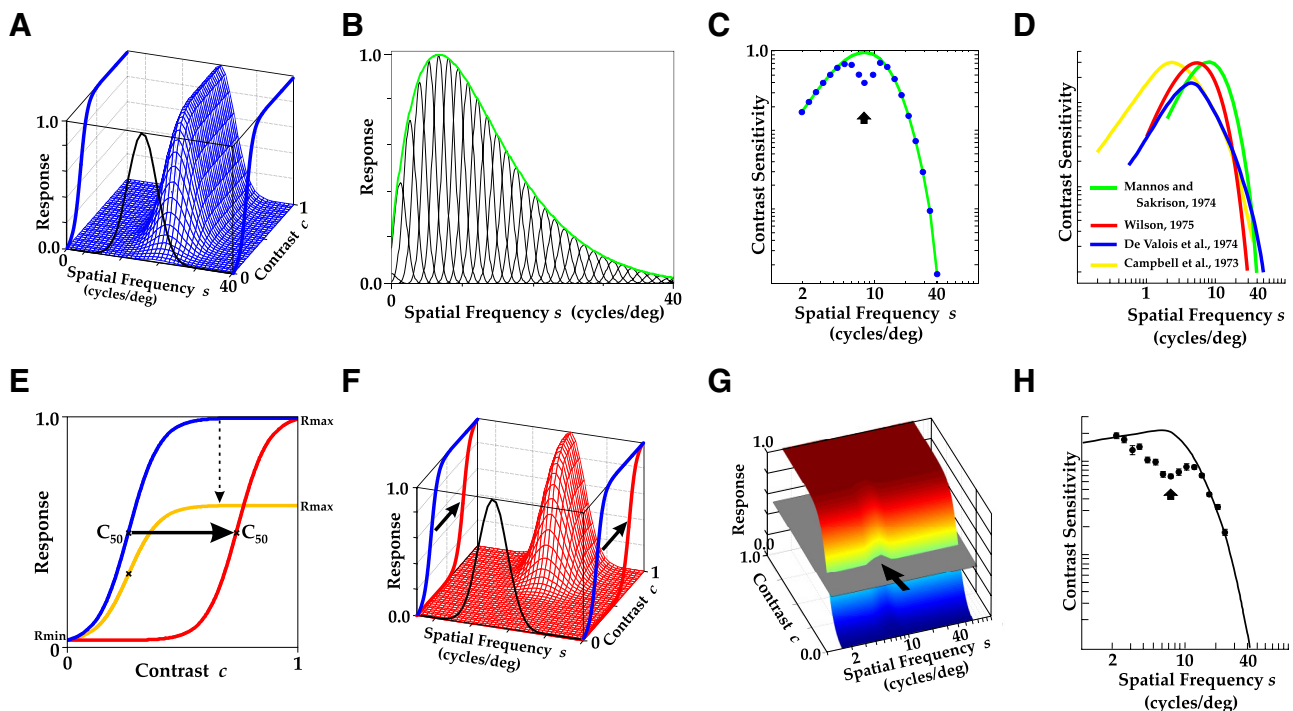


FIG. 1. The organization and operation of the ensemble. *A*: a typical unit. The spatial frequency tuning and the contrast gain function of the unit are shown. *B*: the ensemble. The green line denotes the human contrast sensitivity function (CSF) (Mannos and Sakrison 1974) with which the responses of individual units were scaled. *C*: the CSF of the ensemble before and after adaptation (green line and blue dots, respectively). Arrow denotes the adaptation stimulus. *D*: human CSFs redrawn from previous reports. *E*: the adaptation of a single unit was implemented as an increase in its  $C_{50}$  (horizontal arrow), decrease in  $R_{max}$  (vertical arrow), or both (not shown), relative to the unadapted CGF (blue line). *F*: the tuning profile of the unit shown in *A* after an increase in its  $C_{50}$ . *G*: CGFs of the units in the adapted ensemble. Gray rectangle denotes half-maximal response; the intersection of the rectangle with the CGFs denotes the  $C_{50}$  values of all the units in the ensemble. *H*: human CSF before and after adaptation (line and dots, respectively), after Blakemore and Campbell (1969).

discriminability ( $d'$ ) analysis (Lehky and Sejnowski 1990a, 1999). Contrast threshold at a given test frequency  $s$ ,  $V_s$ , was defined as the contrast  $c$  at which the population response of the ensemble to the test stimulus was larger than its response to the test stimulus at equiluminance at 99% confidence level. The CSF of the ensemble was defined as  $V_s^{-1}$  (Blakemore and Campbell 1969; De Valois and De Valois 1988; Graham 1989).

### Measuring the adaptation bandwidth of the neuronal ensemble

Adaptation bandwidth  $\omega$  was measured using two independent methods. In the  $\omega_{\text{HA}}$  (bandwidth at half-amplitude) method, adaptation bandwidth was measured as  $\omega_{\text{HA}} = (f_h - f_l)/2$ , where  $f_h$  and  $f_l$  are the higher and the lower spatial frequencies at half the maximal observed contrast threshold elevation, respectively (De Valois and De Valois 1988). In the  $\omega_{\text{CF}}$  (bandwidth by curve fitting) method, the contrast threshold elevation function  $V$  (i.e., the inverse of the CSF) was fitted with the curve  $y = h \exp[-0.5 (\theta^2/\sigma^2)]$ , where  $y$  is the model estimate of  $V$ ,  $h$ , and  $\sigma$  are the height and SD of the curve, and  $\theta$  is the difference between the spatial frequencies of the adaptation stimulus and of the test stimulus. The  $\sigma$  of the fitted curve was taken as bandwidth  $\omega_{\text{CF}}$  by this method (Snowden 1991). The  $\omega_{\text{HA}}$  method does not account for changes in the bandwidth due to multiplicative scaling, whereas the  $\omega_{\text{CF}}$  method does (Snowden 1991).

## RESULTS

To investigate the relationship between the adaptation behavior of the system and of the units, we constructed a simple, single-layered, distributed ensemble that processed spatial frequency (Fig. 1) and studied the parameters that affected its adaptation behavior. As in the relevant psychophysical studies (Blakemore and Campbell 1969; Snowden 1991; also see De Valois and De Valois 1988; Graham 1989), the adaptation behavior of the system was assessed using its CSF, which refers to the sensitivity of the system to the luminance contrast of a given test stimulus as a function of its spatial frequency.

It is worth emphasizing at the outset that the neural model in this study was not a detailed simulation intended to capture the complexity of the underlying natural phenomenon in as much realistic detail as possible. Rather our model belonged to a different class of models sometimes referred to as “abstract models” or “demonstrations,” the goal of which is to prove a given principle (Churchland and Sejnowski 1992, p. 136–137; Crick 1988, p. 114). There are many well-known instances of such proof-of-principle models (see, e.g., Lehky and Sejnowski 1990a,b; Minsky and Papert 1987; for additional examples, see Arbib 2002; Bishop 1995; Churchland and Sejnowski 1992; Dayan and Abbott 2001). Our model aimed to demonstrate the potential problems with pattern adaptation as simply and transparently as possible, while remaining relatable to its neurobiological context. That is, our model was intended to best balance computational simplicity with biological plausibility and not necessarily to simulate the details of human spatial frequency processing. It is also worth noting that we did not aim to determine whether spatial frequency channels (Blakemore and Campbell 1969; Braddick et al. 1978; Klein 1992) exist per se, but only to examine whether pattern adaptation could be reliably used to determine if they do.

Each unit in the ensemble was tuned to both spatial frequency and contrast (Fig. 1A). The ensemble consisted of 40 units, the preferred spatial frequencies of which were spaced

uniformly from 0 to 40 cycle/° (Fig. 1B). To help the model simulate the human CSF (Ginsburg 1981; Wilson 1975), the maximum response of each unit was scaled by a quantitative description of the human CSF (Mannos and Sakrison 1974) (denoted by the green line in Fig. 1B), but the contrast tuning (i.e., the contrast gain function or CGF) of the units remained identical across the ensemble (not shown). The units had no properties other than those described in the preceding text. In particular, the units had no cable properties, interconnections or spatiotemporal dynamics. Note that although the model makes no assumptions about the neural substrate of a model unit, a unit can be thought of as an individual neuron, channel (Blakemore and Campbell 1969; Braddick et al. 1978; Klein 1992), “analyzer” (Graham 1989), or some other entity, as appropriate.

The CSF of the ensemble was determined by measuring, in the presence of neuronal noise, the contrast threshold of the ensemble at 20 different test frequencies using discriminability ( $d'$ ) analysis (see METHODS). CSF of the unadapted ensemble (green line; Fig. 1C) was qualitatively similar to that of unadapted humans (Fig. 1D), indicating that the model adequately (although by no means exactly) simulated the human CSF.

Adaptation of the ensemble was implemented as an increase in the  $C_{50}$  or as a decrease in the  $R_{\text{max}}$  of the CGF of a given unit  $i$  (see Fig. 1, E and F) as a function of its response  $R_i$  to the adaptation stimulus

$$\Delta C_{50,i} = f(R_i) \quad (1A)$$

and

$$-\Delta R_{\text{max},i} = f(R_i) \quad (1B)$$

where  $R_{\text{max}}$  is the maximal response of the neuron, and  $C_{50}$  is the contrast that elicits 50% of the maximal response (Albrecht et al. 1984; Kohn and Movshon 2003; Movshon and Lennie 1979; Ohzawa et al. 1982; also see Kohn 2007). In the simplest scenarios, these functions were implemented as the corresponding linear relationships

$$\Delta C_{50,i} = m R_i \quad (2A)$$

and

$$-\Delta R_{\text{max},i} = m R_i \quad (2B)$$

where  $m$  is the arbitrary adaptation gain.

Figure 1G shows the CGFs of the units after the ensemble was adapted to an 8 cycle/° stimulus (arrow) according to Eq. 2A, resulting in an increase in the  $C_{50}$  values of the cells in linear proportion to their responses to the adaptation stimulus ( $m = 2$ ). All other parameters, including all spatial frequency tuning parameters, remained unchanged (not shown). The CSF of the adapted ensemble (blue dots; Fig. 1C) showed that the contrast sensitivity was the lowest (i.e., contrast threshold elevation was maximal) at the spatial frequency of the adaptation stimulus (or adaptation frequency; arrow in Fig. 1C) and was progressively less affected farther away from this frequency. This adaptation behavior was comparable to that reported by Blakemore and Campbell (1969) (Fig. 1H).

Psychophysical studies typically measure the effects of pattern adaptation as the bandwidth of contrast threshold elevation



function because the threshold elevation is expected to be selective to the extent that the underlying pathways are independent (Braddick et al. 1978; Graham 1989; Klein 1992; Westheimer 2001; Wandell 1995). The adaptation bandwidth is generally taken as a measure of the bandwidth of the underlying channel or analyzer (see Graham 1989; Klein 1992; Wandell 1995). We therefore focused our modeling efforts on studying how the adaptation bandwidth at the system level ( $\omega$ ) is affected by the spatial frequency tuning width ( $\sigma$ ) of individual units.

By the conventional bandwidth-at-half-amplitude ( $\omega_{HA}$ ) method of measuring adaptation bandwidth (see METHODS), the adaptation bandwidth of the adapted CSF shown in Fig. 1C was about 4 cycle/deg, which is roughly comparable to those from many previous psychophysical studies at this adaptation frequency (also see following text). Qualitatively similar results (not shown) were obtained for other adaptation frequencies, and when  $R_{max}$  was varied instead of, or in addition to,  $C_{50}$ . Thus, the ensemble was able to adequately simulate the essential features of human pattern adaptation.

Given this, we tested whether and to what extent the adaptation bandwidth of the ensemble depends on the spatial frequency parameters of the underlying units, using three different series of simulations. In the first series, we tested whether the adaptation bandwidth of the ensemble can vary independently of its spatial frequency parameters. To do this, we systematically varied the value of the linear adaptation gain

$m$  while keeping all spatial frequency parameters constant (see Fig. 2A). The adaptation bandwidth of the ensemble measured using the conventional bandwidth-at-half-amplitude method,  $\omega_{HA}$ , varied as a function of  $m$  (gray line; Fig. 2B). When bandwidth was instead measured using the curve-fitting ( $\omega_{CF}$ ) method (see METHODS), which is sensitive to changes in the magnitude of contrast threshold elevation, the bandwidth also varied as a function of  $m$  (black line, Fig. 2B), indicating that this effect was not an artifact of the method we used for measuring the bandwidth. If adaptation bandwidth were solely a function of the spatial frequency parameters of the units, the bandwidth would be expected to remain constant across the various values of  $m$ , because the spatial frequency parameters were held constant. We obtained similar results when  $C_{50}$  varied as a simple nonlinear function of the cell's response to the adaptation stimulus

$$\Delta C_{50,i} = R_i^m \quad (3)$$

(Fig. 2C). Together, these results indicate that an ensemble with the same spatial frequency parameters can produce different adaptation bandwidths. Thus the adaptation bandwidth provided a poor estimate of the spatial frequency tuning width of the underlying units or vice versa.

It should be noted that what the preceding simulation demonstrates is not that the spatial frequency tuning of the units has no effect on the adaptation bandwidth of the ensemble—for our

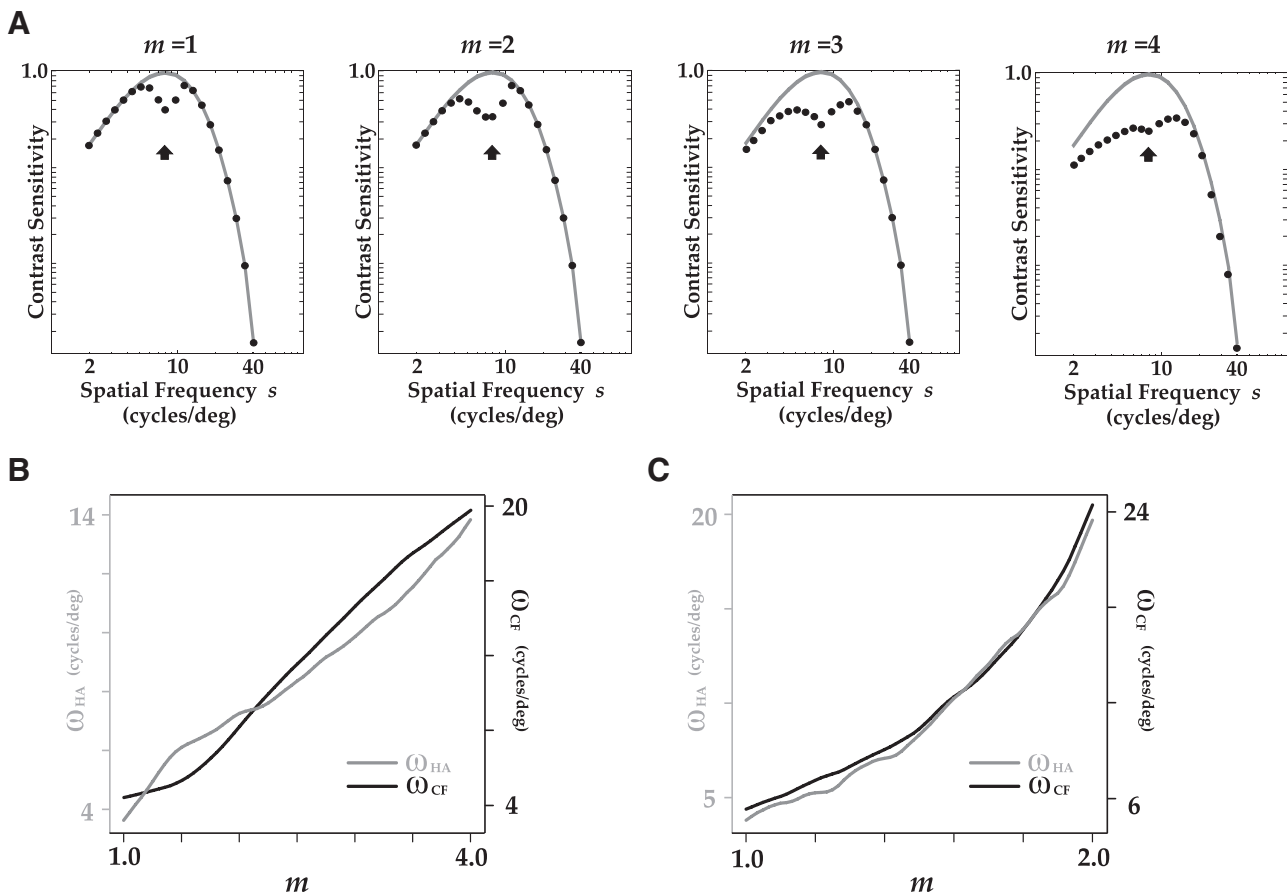


FIG. 2. Variations in the adaptation bandwidth when spatial frequency parameters are unchanged. A: CSF (gray line, unadapted; black dots, adapted) of the ensemble at  $m$  values of 1.0–4.0 in Eq. 2A. B and C: adaptation bandwidths ( $\omega_{HA}$ , left y axes;  $\omega_{CF}$ , right y axes) measured as a function of  $m$  in Eq. 2A (panel B) or Eq. 3 (panel C).

simulations do show that the former can affect the latter (see, e.g., Fig. 1C)—but that other parameters such as  $C_{50}$  and  $R_{\max}$  also can. On the other hand, while the adaptation bandwidth in this particular simulation varied as the sole function of  $C_{50}$  or  $R_{\max}$ , this does not mean that the adaptation bandwidth of the system is solely dependent on these parameters either.

In the second series of simulations, we tested the converse scenario, i.e., whether ensembles with different spatial frequency parameters can produce similar adaptation bandwidths. To do this, we constructed two different ensembles. In the first ensemble, the spatial frequency tuning width  $\sigma$  of each unit was 1 cycle/°, and in the second ensemble, each unit had a  $\sigma$  of 4.0 cycle/°. The two ensembles were identical in all other respects. Figure 3A shows the bandwidths of the two ensembles for various values of adaptation gain  $m$  in Eq. 2A. The two lines were not identical, indicating that spatial frequency tuning of the individual units did affect the adaptation of the ensemble in this case. Nonetheless, the two sets of bandwidths were either largely similar or identical for many values of  $m$ , so that the spatial frequency tuning width could not be unambiguously estimated from the corresponding adaptation bandwidth. Similar results were obtained using the nonlinear adaptation gain in Eq. 3 (Fig. 3B) and when the  $R_{\max}$  values were similarly changed instead (data not shown). Thus ensembles with different spatial frequency parameters can produce similar, sometimes identical, adaptation bandwidths.

It is worth re-emphasizing that what this simulation demonstrates is not that modulating the spatial frequency of the underlying units has no effect on the adaptation of the ensemble but only that there exist scenarios in which these modulations have little substantial effect on the adaptation of the ensemble. In the present case, the reason why this ensemble produces similar bandwidths across a considerable range of spatial frequencies is twofold (unpublished observations): first, while the tuning width manipulations used in this simulation substantially change the overlap between *distant* tuning curves (i.e., tuning curves that peak at substantially different spatial frequencies), they only modestly affect the overlap among *nearby* units. Because adaptation bandwidth is a function of (among other things) the overlap among units near the adaptation frequency, the tuning width manipulations have little effect on adaptation bandwidth in this case. Second, the adaptation gain  $m$  (Eqs. 2A and 2B) was comparatively low so that changes in the magnitude of  $R_i$  brought on by the changes in

the tuning width had a correspondingly smaller effect on the overall adaptation of the ensemble. The point of this admittedly selective manipulation of parameters is solely to demonstrate that there exist scenarios where the adaptation bandwidth of the network is not attributable to a unique tuning width of the underlying units (see DISCUSSION).

In the third series of simulations, we tested whether our ensemble can produce nonselective adaptation. To do this, we systematically varied the correlation coefficient  $r$  between  $\Delta C_{50}$  and  $R$  in Eq. 2A, so that the degree of the adaptation of the units was a noisy, or leaky, linear function of the responsiveness of the units to the adaptation stimulus. Because this added noise was random across units, i.e., the  $\Delta C_{50}$  value of a given unit did not depend on its spatial frequency tuning properties, the resulting CSF had random “dips” at spatial frequencies corresponding to the neuron/s that happened to have a comparatively high  $\Delta C_{50}$  value (data not shown). These dips, which occurred even in the unadapted ensemble, gave the false impression that adaptation was occurring even when it was not or was occurring at spatial frequencies other than the adaptation frequency. Thus, in this ensemble, genuinely adaptation-related decreases in contrast sensitivity were confounded by the noise-related decreases in contrast sensitivity. We therefore averaged out the noise-related effects using two approaches: 1) we determined the CSF as the average CSF over 1,000 independent rounds of adaptation, or 2) we increased the number of units in the ensemble to 400 so that the CSF was much less sensitive to the noisiness of individual neurons. Both approaches yielded similar results (not shown). We present here the results from the latter approach.

Figure 4 shows the CSFs of an ensemble with 400 units at various values of  $r$  while all other parameters were held constant (see legend for details). When  $\Delta C_{50}$  and  $R$  were perfectly correlated ( $r = 1.0$ ), the adaptation was selective, as expected (Fig. 4, *far left*). However, the adaptation of the same ensemble was increasingly nonselective when the correlation was lower, albeit still statistically significant ( $p \ll 0.05$ ;  $df = 398$ ; Fig. 4, *rightmost 3 panels*). When the correlation was 0.7, the ensemble still showed adaptation, but the adaptation was no longer selective in any conventional sense (Graham 1989). Varying the correlation between  $-\Delta R_{\max}$  and  $R$  also yielded similar results (not shown). Thus lack of selective adaptation at the system level does not necessarily mean a lack of selective units at the neural level.

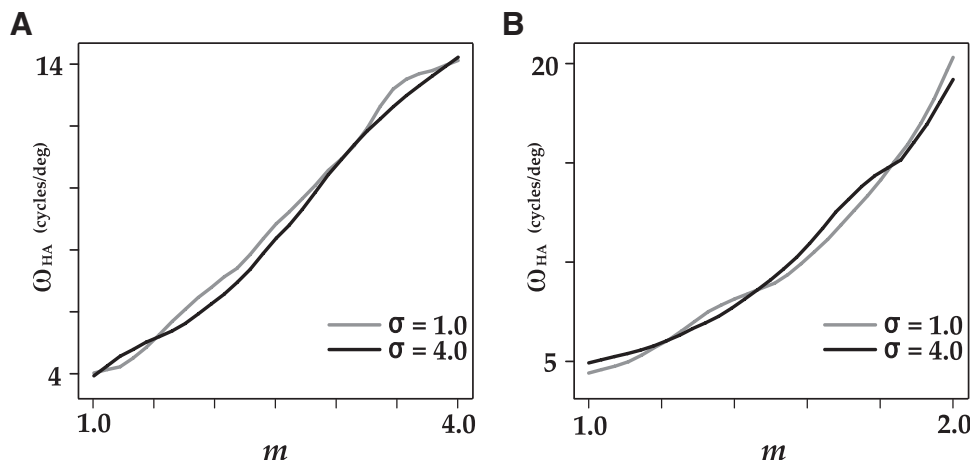


FIG. 3. Adaptation bandwidth of ensembles with different spatial frequency parameters. The adaptation bandwidth ( $\omega_{\text{CF}}$ ) of 2 ensembles, in which the units had tuning widths ( $\sigma$ ) of 1.0 and 4.0 cycle/°, respectively, as a function of adaptation gain  $m$  in Eq. 2A (panel A) or Eq. 3 (panel B).

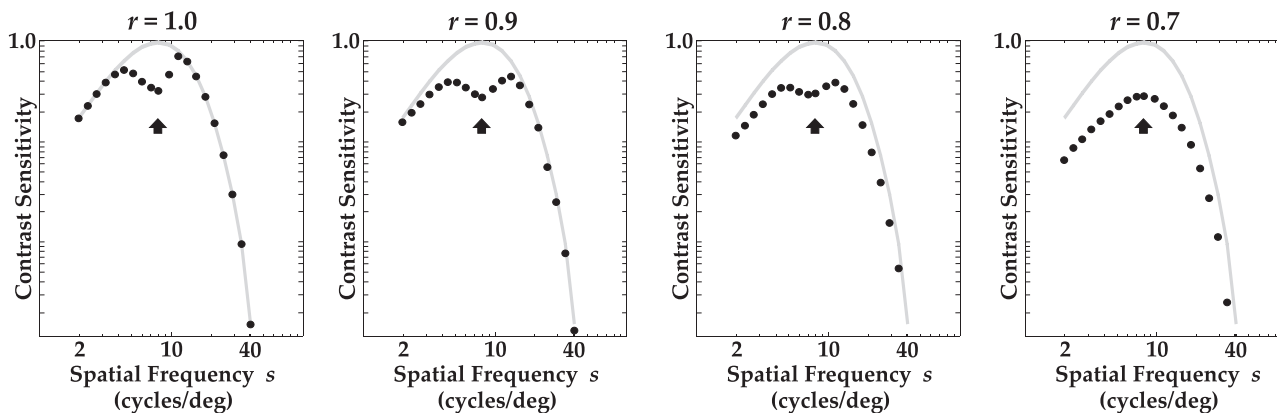


FIG. 4. Adaptation bandwidth as a function of the “leakiness” of adaptation. The correlation  $r$  between  $R_i$  and  $\Delta C_{50,i}$  in Eq. 2A was systematically varied, while all other parameters (400 units, each with  $\sigma = 2.0$  cycle/deg;  $m = 2$ ) were held constant. CSFs for representative values of  $r$  are shown.

## DISCUSSION

Together, the results from the three series of simulations demonstrate, for the first time, that the adaptation bandwidth of the ensemble does not necessarily reflect the spatial frequency tuning parameters of the underlying units, regardless of whether a unit is an individual neuron, or a channel, or some other entity. This is essentially because adaptation bandwidth at the system level is confounded by parameters other than the underlying tuning properties of interest. To the extent that such confounds may apply to other system-level response measures (see following text), our results imply, in a more general sense, that pattern adaptation is not a reliable method for estimating the properties of the underlying units. However, the implication of our study is not that pattern adaptation can serve no useful purpose (see following text), but that its potential uses are severely limited. Similarly, what our results warrant is a thorough re-examination of the relevant previous psychophysical results, and not a wholesale rejection of them.

The notion that pattern adaptation has potential problems is not altogether surprising because the simple mathematical considerations noted in INTRODUCTION indicate as much. The significance of our study lies in demonstrating, using simple and transparent methods, how potentially serious these problems are. Our results show not only that pattern adaptation can be a poor estimator of the underlying neural properties but also that it can readily produce seriously misleading estimates in ways that are not clear from first principles alone. Thus what is surprising about the problems with pattern adaptation is how plausible and varied they are. Judging by the continued use of this technique, the plausibility of these problems has not been fully appreciated heretofore.

### Factors that confound pattern adaptation

To the extent that the adaptation bandwidth of the system is confounded by factors other than the spatial frequency parameters of the units, the problem of using the former to measure the latter is underconstrained or “ill-posed.” This raises the question of whether, in the future, this measurement procedure can be constrained so that the adaptation behavior of the system does reflect the underlying spatial frequency parameters. There are substantial obstacles to doing this as illustrated by the specific problem of estimating the spatial frequency tuning width  $\sigma$  of the units from adaptation bandwidth  $\omega$  of the system. First, as

our results demonstrate,  $\omega$  is a multivariate parameter affected by confounding variables other than  $\sigma$ . Therefore, the confounding variables and the nature of their relationship to  $\omega$  need to be determined independently of pattern adaptation (e.g., using neurophysiological methods), so that the confounds can be quantitatively accounted for. It must be noted in this regard that the confounds demonstrated by our minimalistic model likely represents but a small subset of the actual confounds. Second, even after all the confounds are accounted for, discerning the relationship between  $\omega$  and  $\sigma$  is not straightforward, and involves at least two steps: *step a*, estimating the adaptation-dependent changes in the CGF parameters  $\psi$  (so that  $\psi \in \{C_{50}, R_{\max}, \dots\}$ ) of individual units from a given value of  $\omega$ . Because, as our models indicate, each  $\psi$  parameter can affect  $\omega$  on its own, the relative weight of each  $\psi$  parameter must be independently determined before  $\omega$  can be regressed on  $\psi$ . This still leaves *step b*, which involves estimating  $\sigma$  from the observed changes in  $\psi$ . The neurophysiological relationship between  $\psi$  and  $\sigma$  is largely unknown, and the few available studies (Albrecht et al. 1984; Van Wezel and Britten 2002) indicate that  $\psi$  and  $\sigma$  are largely unrelated. Thus carrying out *step b* requires not only that the relationship between  $\sigma$  and  $\psi$  be studied for all relevant visual areas/regions but also that the  $\sigma$  and  $\psi$  be substantially correlated for all relevant stages of visual processing. Third, note that although  $\sigma$  values were identical across the ensemble in our models, this is unlikely to be the case in the visual system, so that the  $\sigma$  values of individual units (i.e., neurons, channels, etc) must be determined from the point estimate of  $\sigma$  resulting from the preceding exercise. Finally, note that although our results focus, as many pattern adaptation studies do (see Graham 1989), on the problems of estimating  $\sigma$  from  $\omega$ , these concerns likely apply in general to discerning any given neuronal parameter from any given pattern adaptation parameter at the psychophysical level. At the very least, it remains to be demonstrated that they do not.

The preceding considerations mean that pattern adaptation cannot be used to reliably estimate the spatial frequency tuning properties of the underlying units. More generally, they help illustrate the larger principle that system-level response measures cannot be used to estimate the corresponding neuronal parameters, absent compelling evidence that the given system-level measure is a univariate function of the intended neuronal parameter.



### Possible future directions

An important issue not addressed by our study is whether it is feasible to use the pattern-adaptation technique to address the more general question of whether the underlying units are tuned at all to begin with, e.g., whether channels exist. Two lines of evidence indicate that this is also unfeasible. First, we demonstrate that tuned units can produce nonselective adaptation (Fig. 4), so that a lack of selective adaptation cannot be taken to imply a lack of tuned units. But this leaves open a second possibility that when selective adaptation does occur, one can infer that the underlying units are tuned because we were unable to obtain selective adaptation without tuned units (unpublished observations). However, Sawamura et al. (2006; also see Crowder et al. 2006) have demonstrated that in macaque inferotemporal (IT) neurons, adaptation to one stimulus can induce adaptation to a different stimulus. Such cross-adaptation straightforwardly means that the presence of selective adaptation cannot be reliably taken to infer the existence of tuned units (or channels) either.

To the extent our results indicate that adaptation at the system level does not reliably reflect of the properties of the underlying neurons, the use of adaptation in fMRIa experiments (see Grill-Spector and Malach 2001; Grill-Spector 2006) for this purpose needs to be re-evaluated. We emphasize, however, that our results raise questions about interpreting fMRIa results in neuronal terms but not about the technique per se (qv. Crowder et al. 2006; Krekelberg et al. 2006; Sawamura et al. 2006).

Also, while our models do not address the channel theory (Blakemore and Campbell 1969; Braddick et al. 1978; Klein 1992) itself, they do indicate that the support for this theory from pattern adaptation needs to be re-evaluated. To be sure, the channel theory is supported by evidence from many other established psychophysical techniques, including masking and subthreshold summation (Braddick et al. 1978; De Valois and De Valois 1988; Graham 1989; Wandell 1995). However, our results raise the possibility that these techniques are also subject to similar concerns as pattern adaptation. It is conceivable that these potentially shared confounds can be resolved by using these techniques independently of each other to estimate a particular neural parameter of interest, e.g., the tuning width of the spatial frequency channel with a peak at 8 cycle/°. However, the tenability of this approach also remains to be demonstrated, much like the tenability of the pattern adaptation technique by itself.

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