Response Normalization and Blur Adaptation: data and multi-scale model

A dynamic model of contrast and blur adaptation

In all adaptation phenomena, the current state of a system depends on its previous history, but our experiments gave no information about the growth and decay of adaptation over time. The subtractive term $r(\text{adapt})$ in the model represents a steady state, which we presume is reached after sufficient time has been allowed for adaptation to stabilize. Nevertheless, to help us and the reader understand better the model's behavior, its underlying assumptions and future potential, we developed a simple dynamic version, outlined in Fig. S1. We envisage that each channel stores a running average $y$ of its exposure to contrast. This storage is easily implemented by low-pass filtering: $y$ is a temporally smoothed version of filter response $r$. At each moment, a fraction of the stored value is subtracted from the current response $r$, to give the output at time $t_i$: $R_i = r_i - k_y$. The smoothing of $y$, and subtraction of $k_y$ from $r$, combine to make the output $R$ a high-pass filtered version of $r$ (see Fig. S2C for examples). Temporal changes are emphasized and steady values partially attenuated. In our discrete implementation, the 'history' $y_i$ is updated at each time-step $\delta t$, according to a linear rule:

$$y_i = y_{i-1} + w \cdot \delta t \cdot (r_{i-1} - y_{i-1}).$$

In continuous form this corresponds to a simple first-order differential equation, $dy/dt = w(r-y)$. It is easy to see that if $r$ is steady, and $r \neq y$, $y$ will continue to increase or decrease until $r=y$. The mechanism that computes $y$ from $r$ is just a linear, low-pass temporal filter, and behaves exactly as the capacitor in a simple analog RC circuit. The factor $w$ determines how briskly or sluggishly $y$ tracks the value of the input $r$. Higher values of $w$ make $y$ change more quickly, and so $w$ is the inverse of the time constant ($1/w = RC$ in the analog circuit).

An interesting property of capacitors is that they store charge when the circuit is broken. In effect, they memorize the state of the RC system if and when the effective resistance $R$ suddenly goes to infinity (open circuit). The decay time-constant (RC) becomes infinite. Sample-and-hold circuits use this principle for short-term storage of input voltage levels. The exact equivalent in our scheme is that each channel can store its own state $y$ during a blank period by using a simple rule: set $w=0$ when $r=0$, otherwise $w = \text{constant}$. Setting $w=0$ implies $dy/dt=0$, and so $y$ is put on hold indefinitely, until $w>0$ which occurs when input is restored ($r>0$). This simple rule implements the persistence of the pre-adaptation effect that we found was necessary to explain the similarity in results of experiments 1 and
2. Recall that the pre-adaptation idea has two important aspects: (a) observers adapt to the focused world before the experiment begins, and (b) that state of adaptation persists during blank adaptation in the experiment. The storage rule (hold $y$ by setting $w=0$ when $r=0$) achieves just that. Its effect in normal vision is to store the adaptive term $r(norm)$ during a blank period, such that $R(test, blank\_adapt) = r(test) - k.r(norm)$. We saw in the main text that this accounted for the success of the norm-based model, while the absence of such storage [$R(test, blank\_adapt) = r(test)$] explained the failure of the 'fatigue model'. We can now see that in this dynamic form the two models differ only in their temporal update rule for $y$. The fatigue model in effect assumes $w=constant$ at all times, so any pre-adaptation effect decays away during blank periods, while in the norm-based model it is stored. [In practice, capacitors do not store charge forever; it slowly leaks away because of practical imperfections. Analogous leakage is produced in the present model if noise is added to $r$. When $r$ is nominally 0 the presence of non-zero values due to noise in the filter output means that $w$ is not continuously clamped at 0, and the stored value of $y$ slowly decays towards 0.]

**How the dynamic model explains blur adaptation**

Fig. S2 shows how the main features of blur adaptation are captured by the multi-scale subtractive model. It illustrates the norm-based version – i.e. with the 'hold' feature enabled. The success of the model with our steady-state data does not depend at all on the dynamic features shown here, but this dynamic view offers further insight. In Fig. S2A, a sequence of images with different $\alpha$ values is presented (red trace). As in the experiment, all RMS contrast values are matched, except for the period $t = 50$ to $99$ where contrast is 0 (blank). The blue curve (Fig. S2A) shows matching $\alpha$ values that would be selected if the comparison image were presented briefly at time $t$ on the control side of the display. During the pre-adaptation period ($t = 0$ to $49$) matching blur is constant and veridical ($\alpha=0$). At the onset of a sharpened image ($t=100$), the matching $\alpha$ first jumps to the true value ($\alpha=0.5$) but then adapts back towards zero. This is the neutralization or normalization phenomenon, and it is partial as implied by our data, not complete. The same can be seen during the period of exposure to blur ($t=300$ – $399$), while the temporary blurring and sharpening of focused images (Webster et al., 2002) can be seen after exposure to sharpened and blurred images respectively.

In Fig. S2B we show for the same 5 exposure periods how the blur code $b$ varies over time. At the onset of the sharp image ($\alpha = 0.5$), $b$ drops not to -0.5, but to about -1. We can see from Fig. 8 that this is a general effect: adaptation to the norm ($\alpha = 0$, triangles) has the effect of amplifying the value of $b$ for any test image. For this case ($k=0.4$) we have approximately: $b = -2\alpha$. As adaptation to the sharp image progresses (Fig. S2B, $t = 100-199$), $b$ falls back to about -0.5. A closer look at Fig. S2B reveals a
general rule: during a steady exposure period, \( b \) always converges to the same magnitude as \( \alpha \):  
\[ b \approx -\alpha. \]
This occurs because, by design, the stored response values \( y \) for any image \( I \) converge onto the corresponding values of \( r \), as described above. The output values \( R(I) = r(I) - k.y(I) \) therefore converge to \( R(I) = (1-k).r(I) \). In this simple linear system, that is equivalent to a uniform attenuation of contrast by factor \((1-k)\) which does not change the relative activation of different channels and thus leaves \( b \) the same as if no subtraction had occurred. Fig. 8 (diamonds) confirms that with no subtraction, \( b \approx -\alpha. \)

In short, on exposure to blur or sharpness \(|b|\) starts high but if that image slope is maintained, \( b \) adapts (converges) to \( b \approx -\alpha. \)

On this model then it is not adaptation *per se* that causes blur codes \( b \) to change, but rather it is situations where the pattern of response \( r() \) to the current image differs from the adaptation state \( y() \) that cause \( b \) to differ from its fully adapted value. Adaptation leads to high-pass temporal filtering of contrast at the level of individual channels (Fig. S2C), and this causes contrast changes to be emphasized. The net result at the level of blur computation is that temporal changes in blur \( b \) also tend to be emphasized (Fig. S2A,B).

This clearly raises a puzzle. During adaptation, blur codes \( b \) converge towards the adapting value \(-\alpha\), so why do blur matches \( \alpha \) appear to normalize towards 0 over time (Fig. S2A)? The apparent paradox is resolved when we consider that the matching task involves two blur codes – for the test image and the comparison image. The comparison image is always presented after either blank or focused adaptation (and with the storage mechanism in place, these behave in the same way). Thus for the comparison image \( b \approx -2\alpha \text{ throughout} \) but for the adapting image \( b \approx -2\alpha \) only initially. At first their \( b \)-codes will match when their \( \alpha \)-values match – hence a veridical match is made. But as adaptation progresses, the \( b \)-code for the adapter converges to about \(-\alpha\), and so the comparison \( \alpha \) will have to be halved to make the blur codes match again. We can see this in the modeling of Fig. S2A, and we see it in the experimental data of Fig. 10D,E. Adapting and testing to the same \( \alpha \) (+0.5 or -0.5) caused matches to shift towards zero by 0.2 to 0.3 units of slope. This is the (partial) neutralization phenomenon.

Why is there no corresponding shift of perceived blur during adaptation to focused images? Our answer is that the system is already pre-adapted to focused images; hence there is no change in adaptation state \((y)\) during adaptation, and so blur code \( b \) does not change over time. [If there were no pre-adaptation, this stability would remain true, but it would be true for all adapting images, not just focused ones, whereas we find that adapting to blurred or sharpened images makes them appear less blurred, and less sharp respectively.]
How important is the pre-adaptation assumption? We saw in Fig. 9 that without it the predictions for experiment 1 were hopeless. The key factor, in our view, is the existence of a storage mechanism that serves to maintain the state of adaptation during blank periods. Fig. S3 gives some more insight. Without storage, the normal state of adaptation decays during blank periods (Fig. S3C, dashed curves, \( t=50-99 \)). At the onset of the sharpened image, following a blank period, \( b \) immediately attains its final state (Fig S3A). Even though the channels are adapting, they do so in concert (Fig. S3C), thus attenuating effective contrast, but \( b \) does not change over time and the neutralization effect is (incorrectly) absent. Thereafter \( (t>200) \), the blur codes \( b \) for the adapter do change over time; channel responses (Fig. S3C) and blur codes (Fig. S3B) are identical to the norm-based model (Fig. S2) because no blanks are involved. But the comparison image must again be considered. In Figs. S2 and S3 we have taken the control adapter to be blank, as in experiment 1. Hence, with no storage, \( b\approx -\alpha \) (Fig. 8), rather than \( b\approx -2\alpha \), and this makes a large difference to the outcome. At the onset of blur \( (t=300) \) the matching \( \alpha \) is far too extreme, and after a period of adaptation a 'correct' match \( (\alpha = -0.5) \) is achieved – but neither of these outcomes matches the data. All of these errors correspond with what we saw in Fig. 9, but are perhaps more clearly grasped with the aid of Fig. S3. The importance of the pre-adaptation and storage assumptions is confirmed.

**Supplementary Discussion**

**Norms at multiple time scales**

We have seen that a critical requirement for predicting the aftereffects was the assumption that the channels are pre-adapted over long timescales to the spatial structure of natural scenes, and that the mechanisms held this memory even when an adapting stimulus was “absent” (for the blank field). This has close parallels to color coding. Color appearance is pre-adapted to the average long-term spectra of the observer’s environment. If it were not, achromatic settings should drift arbitrarily as observers dark adapt and should diverge between the fovea and periphery because of the differences in spectral sensitivity. Instead they remain remarkably stable (Webster & Leonard, 2008), and require long periods to readjust when the spectral sensitivity of the observer changes, for example following cataract surgery (Delahunt, Webster, Ma, & Werner, 2004). This suggests that there may be at least two important components to adaptation – a long-term adjustment that reflects the underlying intrinsic sensitivity of the visual system, and a short-term adjustment that is instead controlled more extrinsically by the currently viewed stimulus (Webster, Werner, & Field, 2005). There is now substantial evidence for adaptation over multiple timescales (Clifford et al., 2007; Fairhall, Lewen, Bialek, & de Ruyter Van Steveninck, 2001; Kohn, 2007; Vul, Krizay, & MacLeod, 2008). The fact that
these may be manifest in very similar ways in domains as diverse as color appearance and blur perception suggests that they may be a common characteristic of norm-based coding.

Note that the model we developed (Fig. S1) implicitly has a different form of normalization at the longer time scale: we set the gain $g$ of each channel such that filter response amplitudes $r$ would be the same across scales $s$, for $1/f$ images (Brady & Field, 1995; Field, 1987; Field & Brady, 1997).

Ullman & Schechtman (Ullman & Schechtman, 1982) described an elegant and simple adaptive rule in which small, automatic adjustments to gains over time would maintain constancy of average output across channels, as suggested by Georgeson & Sullivan (Georgeson & Sullivan, 1975). Adjustment of $g$ played no part in the successful blur models here, and simple gain adjustment did not predict the data well (Fig. A1), but appropriate prior setting of $g$ may be important in human vision and in the model.

One possibility is that these gain adjustments take place over a longer time-scale than most laboratory adaptation experiments. Consistent with this, Kwon et al. (Kwon, Legge, Fang, Cheong, & He, 2009) showed that four hours of exposure to a reduced-contrast world produced significant enhancements in contrast detection and discrimination and in the fMRI response to contrast. The best-fitting model for this change was a 30% increase in overall response gain, equivalent to $g$ in Fig. 6. This is what we should expect if gains $g$ adapt (normalize) very slowly, while the subtractive adaptation or its CGC equivalent (eqn. A2) modulates responses more quickly.

**Limitations of the dynamic model**

An obvious objection to the 'hold' mechanism in our model is that recovery from adaptation to images or gratings should never occur during blank periods, but for gratings it clearly does (e.g. (Greenlee, Georgeson, Magnussen, & Harris, 1991). It may be that adaptation to focused images (the norm) is very long-lived, but in our model the rate of change ($w$) was constant (except when forced to 0) and this assumption of constant rate is probably incorrect. Greenlee et al. (1991; their Fig. 8) found that the time to recover from grating contrast adaptation increased roughly in proportion to the time spent adapting. The source of this effect is not well understood, but a reasonable extrapolation is to suppose that a lifetime of exposure to focused images would lead to a very long-lasting adaptation state, while short periods of experimental adaptation are short-lived. The dynamic model needs further elaboration to incorporate such variable, history-dependent dynamics. (See, for example, the work of van de Grind et al. (2004) on a divisive gain-control model for the dynamics and storage of the motion aftereffect).
Supplementary References


Supplementary Figures

**Figure S1.** A sketch of the dynamic version of the multi-scale model for blur adaptation. There were 7 filter scales, at 4 orientations (not shown). Strength of adaptation is controlled by factor $k$. Blur is coded from the way response $R$ rises or falls across scales. See text for details.
Figure S2. Shows how the main features of blur adaptation are captured by the multi-scale subtractive model. Three panels illustrate 3 levels of detail for the same sequence of images, divided into 5 periods with different degrees of sharpening or blurring. A: image sequence is defined by $\alpha = 0, +0.5, 0, -0.5, 0$ (red trace); predicted $\alpha$ matches (blue curve). B: Blur codes $b$ vary over time (blue curve); actual spectral slope offset (red trace) is expressed here as $-\alpha$ (to have the same sign as $b$). Variation in the across-scale pattern of stored responses $y$ over time is summarized by computing a blur code for it (green curve). C: Response $R_{av}$ over time, for 3 different filter scales (solid curves), and the corresponding adaptive term $k.y$ (dashed curves). Note how $k.y$ persists during the blank period ($t=50$ to 100) even though responses $R_{av}$ drop to 0.
Figure S3. Like Fig. S2, except that the 'fatigue' model was used, differing from the norm-based model in just one way – its lack of storage of the adaptation state during blank periods. This difference, which mainly affects responses to the comparison stimulus when the control adapter is blank (experiment 1), has a large (and incorrect) effect on the predicted $\alpha$ matches. In panel C, note how the adaptive term $k_y$ (dashed curves) decays to 0 during the blank period ($t=50$ to 100), quite unlike Fig. S2C where storage occurs.