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Vision Research 48 (2008) 2485-2491

Contents lists available at ScienceDirect





journal homepage: www.elsevier.com/locate/visres



Speed adaptation as Kalman filtering

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ARTICLE INFO

Article history: Received 14 April 2008 Received in revised form 13 August 2008

Keywords: Motion adaptation Speed perception Speed discrimination Kalman filtering Bayesian model

ABSTRACT

If the purpose of adaptation is to fit sensory systems to different environments, it may implement an optimization of the system. What the optimum is depends on the statistics of these environments. Therefore, the system should update its parameters as the environment changes. A Kalman-filtering strategy performs such an update optimally by combining current estimations of the environment with those from the past. We investigate whether the visual system uses such a strategy for speed adaptation. We performed a matching-speed experiment to evaluate the time course of adaptation to an abrupt velocity change. Experimental results are in agreement with Kalman-modeling predictions for speed adaptation. When subjects adapt to a low speed and it suddenly increases, the time course of adaptation presents two phases, namely, a rapid decrease of perceived speed followed by a slower phase. In contrast, when speed changes from fast to slow, adaptation presents a single phase. In the Kalman-model simulations, this asymmetry is due to the prevalence of low speeds in natural images. However, this asymmetry disappears both experimentally and in simulations when the adapting stimulus is noisy. In both transitions, adaptation now occurs in a single phase. Finally, the model also predicts the change in sensitivity to speed discrimination produced by the adaptation.

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1. Introduction

The responses of sensory neurons habituate in a characteristic way to maintained stimulation. Such adaptation process may serve to enhance sensitivity to small variations in the environment (Bex, Bedingham, & Hammet, 1999; Clifford & Langely, 1996; Clifford & Wenderoth, 1999; Greenlee & Heitger, 1988; Regan & Beverley, 1985). Every time the environment changes, a new process of adaptation begins. If the purpose of adaptation is to fit sensory systems to different environments (Laughlin, 1989; Thorson & Biederman-Thorson, 1974), it may function as an optimization of the system. This optimization may put responses of the system in the middle of the range for natural images, such as to encode as many stimuli as possible (Grzywacz & de Juan, 2003). Optimization may also mean finding the best condition of the system to perform a task (Atick & Redlich, 1992; Balboa & Grzywacz, 2000a, 2000b; Field, 1994; Grzywacz & Balboa, 2002; Srinivasan, Laughlin, & Dubs, 1982). In either event, to know what optimum is, the system must be able to estimate the statistics of the environment. For example, when one is driving in daylight and suddenly gets into a tunnel, a transient visual impairment occurs. This is because just

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before entering the tunnel the parameters of our visual system are set to daylight, the current state of the environment.

To estimate the new stimulus statistics optimally, engineers would use a Kalman-filter strategy. This filter performs the estimates based on two factors. The first is the quality of the current measurements, and the second are the measurements from the past. If the system knows that current measurements are excellent, then it trusts them. However, if the measurements are of poor quality, then the system has to take more measurements and in the meanwhile, uses those from the past. For example, the system has to be sure that the low light levels found when it gets into a tunnel are due to an actual change of the environment and not to a particular "dark image" of the previous one. The Kalman filter is the optimal way to combine the actual measurements with those from the past. Recently, Grzywacz and de Juan (2003) applied this theory to retinal contrast adaptation and showed that its time course in ganglion cells follows characteristics that are consistent with Kalman filtering.

We wondered whether Kalman-filter strategies are also applied to the adaptation processes in visual perception. In this article, we report on a study of the particular case of speed adaptation. We studied speed adaptation, because, in addition to the well-known importance of motion processing in vision, we now possess enough background knowledge to approach this topic. Recent investigations suggested that perceived speed decreased during adaptation

^{0042-6989/\$ -} see front matter \circledcirc 2008 Elsevier Ltd. All rights reserved. doi:10.1016/j.visres.2008.08.011

to high speeds and followed an approximately exponential time course (Bex et al., 1999; Hammet, Thompson, & Bedingham, 2000). Moreover, as argued by many before (Ullman & Yuille, 1989; Weiss & Adelson, 1998), the distribution of speeds in natural images has a bias towards slow speeds (Martinez Rach, Martinez Verdú, Grzywacz, & Balboa, 2005). It turns out that this distribution, when applied to Kalman filtering, makes surprising predictions for the time course of speed adaptation. The model predicts that the time course of speed adaptation will be different if the speed transition occurs from slow to fast versus from fast to slow. In the Kalmanmodel simulations, this asymmetry would be due to the prevalence of low speeds in natural images. Interestingly, the model also predicts that this asymmetry will disappear if the adapting stimulus is sufficiently noisy. This is because the system does not trust in the current measurements. The model also accounts for more general aspects of motion processing such as the enhancement of sensitivity for speed discrimination as a result of adaptation (Bex et al., 1999; Clifford & Langely, 1996; Clifford & Wenderoth, 1999; Greenlee & Heitger, 1988; Regan & Beverley, 1985). This work on Kalman modeling of the speed-adaptation system appeared previously in abstract form (Barraza & Grzywacz, 2006).

2. Models and simulations

Fig. 1 shows a schematic of the Kalman theory of sensory adaptation. The model begins with the idea of Grzywacz and Balboa (2002) for how a sensory system adapts optimally to an environment when knowing its statistics (Boxes 1–4). In this model, an adaptive stage (Box 1) processes the sensory input and feeds a second stage (Box 2) to obtain the system's responses. Next, the system has to estimate with how much error these responses code important attributes from the environment (Box 3). The system then adapts the preprocessing stage such as to minimize this error (Box 4). To estimate the error, the system needs to know the statistics of the environment. Grzywacz and de Juan (2003) used the Kalman framework to address how the system estimates those statistics as the environment changes. They proposed that the system estimates them from its own responses (Box 5) and from predictions based on past responses (Box 6). Such estimates do not change if current responses are statistically consistent with these predictions. Otherwise, the estimates change slowly, optimally balancing these responses with the tendency of the environment to remain stable.

To perform simulations of the Kalman mechanism, we applied to speed adaptation the theoretical framework developed by Grzywacz and de Juan (2003). If speed adaptation were a form of Kalman filtering, then the sensory system would store the following four types of knowledge to perform the tasks optimally:

(1) One type would be about the relevant statistics of the environment, which in Bayesian formulation, is the prior-probability function. The probability function $P(I|\Lambda)$ indicates the distribution of an input variable of interest when the environment is Λ . Because in our case, the attribute of the environment of interest is speed, $P(I|\Lambda)$ represents the distribution of local speeds in natural images produced by the current environment. From measurements of the distribution of speeds in natural movies, we approximate $P(I|\Lambda)$ with a power law (Dong & Atick, 1995; Martinez Rach et al., 2005), as follows

$$P(I = s|\Lambda = s_k^*) = \frac{1}{s^n + s_k^{*n}},$$
(1)

where *s* is local speed, s_k^* is the estimated mean speed in the environment at time *k*, and *n* is a constant, which was 2.8 in



Fig. 1. Schematics of the Kalman theory of sensory adaptation. The adaptive stage (Box 1) processes the sensory input and feeds a second stage (Box 2) to obtain the system's responses. Next, the system has to estimate with how much error these responses code important attributes from the environment (Box 3). The system then adapts the preprocessing stage such as to minimize this error (Box 4). To perform the error estimation, the system must first estimate the state of the environment (Box 5). The system does this by combining its own responses (Box 2) and the predictions based on responses from the past (Box 6).

our simulations. In other words, we specify the environment here with the mean of its local speeds.

(2) Another necessary type of knowledge is about how the environment changes. This is a second type of prior-probability function, but instead of saying what the statistics of the environment are, this function specifies how rapidly they change in time. Because there are no data available on this yet, we assume that this probability is Gaussian (Grzywacz & de Juan, 2003), i.e.,

$$P(\Lambda_k = s_k^* | \Lambda_{k-1} = s_{k-1}^*)$$

= $\frac{1}{\sqrt{2\pi}((t_k - t_{k-1})/\tau)} \exp\left(-\frac{(s_k^* - s_{k-1}^*)^2}{2((t_k - t_{k-1})/\tau)^2}\right),$ (2)

where τ is similar to a time constant for a typical variation of the mean speed during $t_k - t_{k-1}$.

(3) Knowledge on how information is processed by the system (mainly at Boxes 1 and 2) must be stored and is called the likelihood function. The use of the likelihood function implies that adaptation is a constrained optimization, with limitations coming from the available biological hardware. The likelihood function of the measurement stage, $P(R|I,A_k)$, indicates the probability of responses R when the input is I, with A_k being a set of parameters, indicating the adaptation state of the system. For choosing this function for our simulations, we assumed that perceived speed arose from a process of antagonistic comparison of responses of two temporal filters, one low-pass and one broadly tuned band-pass (Smith & Edgar, 1994). The ratio of the mean responses of these temporal filters increases with temporal frequency (or in our case, with speed) in a sigmoidal fashion (Smith & Edgar, 1994). In this paper, *R* is a statistical sample

of this ratio. We then modeled $P(R|I,A_k)$ with a Gaussian function of R, representing the assumption that the noise was normal and additive. Although it was suggested that noise should be multiplicative because speed perception follows a Weber's law, it is known that this behavior may also be explained by an underlying compressive response with constant noise (Georgeson & Meese, 2006; Johnson, Hsiao, & Yoshioka, 2002; Katkov, Tsodyks, & Sagi, 2006, 2007a, 2007b; see also for discussion Klein, 2006, 2007; Kontsevich, Chen, & Tyler, 2002). For simplicity, we assumed additive noise and expressed the likelihood function as

$$P(R = R_k | I = s, A_k = \gamma_k)$$

= $\frac{1}{\sqrt{2\pi\sigma}} \exp\left(-\frac{(R_k - (\gamma_k s/(1 + \gamma_k s)))^2}{2\sigma^2}\right),$ (3)

where σ is the standard deviation of the noise and γ_k is a parameter of the sigmoidal function (the second term of the numerator of the exponential) representing the mean ratio. This parameter specifies the adaptational state of the system and thus, can vary as the environment changes. The choice of the sigmoidal function is not relevant for the functioning of the model. We tried other curves such as a Weibull function obtaining the same result.

(4) The final piece of knowledge that we must specify is the loss function $L(I,R; \Lambda_k, A_k)$. This function describes how much penalty the system incurs if its response is R when the input is I. The response provides an estimate of the input, but may deviate from a reasonable value because of noise Eq. (3). In this case, the estimate is bad and the system pays a (natural selection) penalty. We assume that the goal of adaptation is to maximize sensitivity by putting the system in the middle of the range of speeds in natural images. In other words, we assume that R provides the most amount of information possible about I. Therefore, we can write the loss function as (for details see Grzywacz & de Juan, 2003).

$$L(I = s, R = R : \Lambda = s_k^*, A_k = \gamma_k) = -\log\left(\frac{P(R|s, \gamma_k)}{P(R|s_k^*, \gamma_k)}\right).$$
(4)

With these pieces of knowledge, one can apply the mathematical machinery of Kalman adaptation (Grzywacz & de Juan, 2003). We were especially interested in the application to the cases where speeds changed abruptly from slow to fast and vice versa. Our interest was so, because the distribution of speeds in natural images had a bias towards low speeds Eq. (1). Hence, adaptation to those two speed transitions could show an asymmetry (Grzywacz & de Juan, 2003). Fig. 2 shows the result of the simulations for these speed transitions.¹ When the adapting speed changes from slow to fast, the model predicts that the time course of adaptation presents two phases, namely, a rapid decrease followed by a slower phase. In contrast, when the change occurs from fast to slow, the adaptation appears to happen in a single phase. Grzywacz and de Juan (2003) explained the reason for this particular form of adaptational asymmetry with further simulations. Their explanation was based on making a transition in an environment with a bias (in our case, towards low speeds). If the transition is away from the bias, then the new measurements are significantly different from the old ones. However, if the transition is towards the bias, the statistical distri-



Fig. 2. Results of model simulations for both transitions (slow-to-fast and fast-toslow) and for noise-free stimuli. The left panel shows an initial fast decay of the speed bias followed by a slow decay. In turn, the right panel shows that the speedbias rise occurs in a single phase.

bution of responses does not change much. Therefore, in the first case, one can trust the new measurements as indicating a change of environment. The system can thus quickly vary the internal adaptational and environmental parameters Eqs. (1) and (3). However, in the second case, one cannot trust the measurements and thus, must make the variations slow, weighing more the past Eq. (2). The reason for the two phases in the first case is that after the system adapts quickly because of the measurements, it becomes conservative, trusting the past. In contrast, in the second case, the system is conservative from the beginning.

To test these explanations of the asymmetry of Kalman speed adaptation, we added noise to the input signal (see Section 3). Our rationale for adding noise was that if the model did not trust the noisy measurements, then the adaptation would have to trust the past. In that case, the slow-fast transition would now cause



Fig. 3. Results of model simulations for noisy stimulus. Plots show that with noise, adaptation occurs in one phase for both transitions.

¹ For this figure, parameters were $\tau = 10 \text{ s}$ and $\sigma = 0.1$, which give adaptation behavior similar to that observed in the psychophysics (see below). Although other parameters change the quantitative behavior, they do not change the qualitative results.

adaptation to develop in a single phase. Fig. 3 shows that this is exactly what the model predicts. However, although the speed of adaptation in this case is a little slower than the fast phase obtained without noise, according to our hypothesis, we expected that it were closer to the slow than to the fast adaptation phase.

Finally, we run simulations to study how the sensitivity to speed changes varies with adaptation (Bex et al., 1999; Clifford & Langely, 1996; Clifford & Wenderoth, 1999; Clifford, 2002). Fig. 4a shows the results of the simulation. The model predicts a maximum discrimination threshold just after the speed change and that it decreases as the system adapts to the new situation.

Consistently with Bex et al. (1999), the model also predicts a linear relation between discrimination threshold and perceived speed (Fig. 4b). Note that this linearity appears with two different slopes corresponding to both adaptations phases. The line with smaller slope (Weber fraction about 0.095) corresponds to the slow



Fig. 4. Model simulations for speed discrimination. (a) Speed discrimination threshold as a function of adaptation time. The plot shows that adaptation enhances sensitivity to speed changes. (b) Speed discrimination threshold as a function of normalized speed. The threshold is expressed as a proportion of normalized speed. The plot shows that there are two Weber fractions corresponding to both adaptation phases. The line with smaller slope (Weber fraction about 0.095) corresponds to the slow adaptation phase. On the other hand, the steeper line (Weber fraction about 0.21) corresponds to the fast adaptation phase.

adaptation phase, and the steeper line (Weber fraction about 0.21) corresponds to the fast adaptation phase.

3. Psychophysical test

To test the model predictions, we performed a psychophysical experiment in which we measured speed bias and discrimination thresholds as a function of adaptation time. We define speed bias as the ratio between perceived and standard speeds. The bias was measured for the four situations simulated with the model.

3.1. Methods

Experimental stimuli were drifting vertical sinusoidal gratings of 1 c/deg and 80% contrast moving to the right. They were presented in two rectangular patches located to both sides of the fixation point on the center of a high-resolution CRT monitor with a 60 Hz refresh rate. The size of the patches was 4 deg and their centers were 2.5 deg away from the fixation point. The mean luminance of the screen was 30 cd/m². The adaptation stimuli were displayed in the left patch, while the right patch contained the standard stimulus for speed comparison. Differently from previous studies on speed adaptation, in this experiment, we used two adapting conditions. In each trial, subjects were first fully adapted to a "pre-adaptation speed" during 60 s. Once the subject was adapted, we changed the speed of the left patch to the "adaptation speed," while the right patch remained with the pre-adaptation speed. The duration of this second part of the stimulus presentation, i.e., the duration of adaptation, was the independent variable of the experiment. Next, we removed the stimuli from both patches and waited 100 ms before presenting test (left) and standard (right) stimuli during 300 ms. Fig. 5 shows schematically the sequence of stimuli presentation in a trial. Importantly, this procedure allows us to isolate the effect of contrast adaptation on the speed bias. Perceived contrast falls with adaptation (Blakemore, Muncey, & Ridley, 1973; Georgeson, 1985; Hammett, Snowden, & Smith, 1994) and perceived speed itself changes with contrast (Stone & Thompson, 1992; Thompson, 1982). In our experiment, both patches contained the grating during the whole sequence of stimulus presentation; therefore, contrast adaptation affected both retinal areas equally.

The noisy-adaptation modification of the stimuli consisted of adding noise to the speed of the grating. The speed switched every three frames between 0.2 and 1.8 of the speed of adaptation.

We instructed subjects to fixate on the center of the screen during the whole presentation of the pre- and adaptation stimuli. Immediately after these stimuli were removed, a short beep



Fig. 5. Sequence of stimulus presentation. The upper plot shows the order of presentation of pre-adaptation, adaptation, and test stimuli on the left patch. Simultaneously, only pre-adaptation and standard stimuli are displayed on the right patch, such as shown in the lower plot. The duration of the pre-adaptation stimulus in the left patch is 60 s. In the right patch, this duration is longer and depends on the duration of the adaptation stimulus. Importantly, we assumed that the system gets fully adapted during the 60 s. Therefore, the state of adaptation before presenting the standard stimulus in the right patch and the adaptation stimulus in the left patch would be the same. Our data below justifies the assumption of full adaptation in 60 s.

sounded so that the subject was prepared for test presentation. The subject task was to indicate by pressing a button of the mouse which stimulus, left or right, moved faster. We used a forced choice paradigm with the method of constant stimuli to obtain the subjects' psychometric functions. We calculated the matching velocity and the discrimination threshold by fitting cumulative Gaussian curves to these functions. The matching velocity corresponded to their 50% point, while discrimination thresholds were calculated from the difference between the velocity at 75% performance and the matching velocity. To obtain these functions, we used a set of six stimuli in each of two blocks of trials. Each stimulus appeared 15 times per block.

Two subjects experienced in motion experiments participated in this experiment, one of the authors and another naïve as to the purpose of the study. Subjects viewed stimuli binocularly and with natural pupils.

3.2. Results

Fig. 6 shows the results for all experimental conditions. Panels A and B (upper row), and Panels C and D (lower row) correspond to the "no-noise" and "noise" conditions, respectively. Figures A and C (left column) correspond to the data obtained with a pre-adaptation speed of 1 deg/s and an adaptation speed of 6 deg/s. Panels B and D (right column) correspond to the data obtained with a pre-adaptation speed of 6 deg/s and an adaptation speed of 1 deg/s. In both cases, the speed of the test was the same as the adaptation speed. Each panel contains adaptation data for both

subjects. Results show that speed adaptation presents two phases when speed changes from slow to fast (Panel A). For the opposite speed transition, adaptation occurs in a single phase (Panel B), as predicted by the model (Fig. 2). When we apply noise to the adapting stimulus, adaptation occurs in a single phase in both cases (Panels C and D), which is also consistent with model predictions (Fig. 3).

We wanted to test whether speed bias decreases with two time constants in Panel A and with a single one in the other conditions. Hence, we re-plotted the data so that they varied linearly with time and the inverse of the time constant was the slope of the lines. In Fig. 7, Panels A and C, we plot $\ln(s - A) - \ln(B)$ as a function of time, where s is the speed bias and A and B are the constants of the exponential decay $s = A + Be^{-t/\tau}$. In Panels B and D, we plot $\ln(B) - \ln(A + B - s)$ as a function of time, where s is the increasing exponential $s = A + B(1 - e^{-t/\tau})$. The constants A and B were obtained by fitting the exponential curves to the experimental data with a least-squares procedure. For the case of the double exponential, we performed the fit separately for each section of the curve. Fig. 6 shows that for the slow-to-fast transition, the time course of speed adaptation presents two exponential time constants when the stimulus is noise-free (Panel A). The fast time constants are 2.0 and 1.3 s for Subjects MC and JB, respectively. In turn, the slow time constants are 18 and 17 s. However, these times constants become a single one when the adapting speed is noisy (Panel C). Our estimates for the time constants in this condition are 13 and 9.2 s for MC and JB, respectively. It is important to note that psychophysical data for the noise-free situation match



Fig. 6. Results of the psychophysical experiments. Each panel shows the speed bias as a function of time for one experimental situation and both subjects. The top panels show the results for the noise-free situation. The top-left panel shows that for slow-to-fast transition, the bias presents two temporal phases, such as those found with model simulations. On the other hand, results show that the bias occurs in a single phase for the fast-to-slow transition (top-right panel). As predicted by the model, when we apply noise to the stimulus, the bias occurs in one phase for both transitions (Bottom panels).

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Fig. 7. Data of Fig. 6 plotted semi-logarithmically. In these plots, we present the exponentially varying data of Fig. 6 in linear form. In it, the slope of the lines is the inverse of the time constant of the exponentials. One can see that only data of the top-left panel presents two time constants. This indicates that in this situation, adaptation occurs in two phases. The bottom-left panel shows that when one adds noise, these two phases become one. The new decay has a single time constant that is intermediate between the two phases of the top-left panel. The two right panels show that for both conditions of the fast-to-slow transition, adaptation occurs with one time constant.

both qualitatively and numerically the model predictions. However, when noise is added to the stimulus, psychophysical data and simulations agree only qualitatively since, in both cases, the time constant of the single phase falls between the fast and slow phases obtained without noise. A numeric discrepancy can be noted in the fact that the time constant of the single phase obtained experimentally is close to the slower phase obtained



Fig. 8. Speed discrimination threshold as a function of adaptation time for both observers. The plot shows that, consistently with the model simulation, the discrimination threshold decreases as the adaptation time increases.

without noise, while for the simulations the time constant is close to the faster noise-free phase (Figs. 2 and 3). Finally, for the fast-toslow condition, Panels B and D show that speed adaptation occurs in a single phase for both noise-free and noisy stimuli, respectively. The mean time constants were 5.9 and 5.3 s for the noise-free and noisy conditions, respectively. Hence, differently from the slow-tofast condition, noise did not affect the fast-to-slow condition significantly. In the simulations, noise increased the time constant of the adaptation in the slow-to-fast condition by about 40% (Fig. 2). In terms of our human data, this effect would be to increase the time constant from about 5 to about 7 s.

Fig. 8 shows the discrimination threshold as a function of adaptation time for both observers, for the slow-to-fast transition. Results show that the threshold decreases with increasing adaptation time in a similar manner to that predicted by the model in Fig. 5.

4. Discussion

In this article, we studied whether speed adaptation followed an optimal Kalman-filtering strategy. We began by modifying the model developed by Grzywacz and de Juan (2003) to deal with speeds. We then performed simulations to generate predictions about speed adaptation. The model predicted that the time course of speed adaptation was different depending on whether the speed transition was from slow to fast or from fast to slow. In the first case, modeled perceived speed presented a maximum immediately after the transition. The predicted perceived speed then decreased in two phases, a rapid fall followed by a slower one. In contrast, when the transition was from fast to slow, the model predicted that the time course would have a single phase. Interestingly, when noise was applied to the adapting stimulus, predicted adaptation occurred in a single phase for both transitions. The model gains generality by predicting also the effect of adaptation on sensitivity to speed changes: the speed discrimination threshold decreases with increasing adaptation time.

Psychophysical experiments showed that those predictions were qualitatively correct and suggested that speed adaptation was optimal in the human visual system. That speed adaptation appears to be optimal makes us think that other brain processes can follow the same strategy. In this context, predictions for other forms of adaptation will strongly depend on the priors. For example, an asymmetric prediction such as that shown in Fig. 2 requires an asymmetric prior. Consequently, it should be applicable also to contrast adaptation (Balboa & Grzywacz, 2003), but not perhaps to light adaptation. This is because the distribution of illuminations in natural environments has no especial bias towards low or high values.

The predictions were not correct in full quantitative details, however. For example, the model predicted a shorter time constant than observed when adding noise to the slow-to-fast condition. Furthermore, in the opposite condition, we could not detect a lengthening of the time constant with noise. This latter detection failure might have been due to inter human-variability, but the former failure was not. We do not believe that these small quantitative failures have to do with the human visual system not using a Kalman-adaptation strategy. Without this strategy, one cannot easily account for the qualitative predictions of asymmetry and of the effect of noise. Rather, the failures of the quantitative predictions are probably due to an imperfect choice of the model Eqs. (1)-(4). We have good data to back up the use of Eqs. (1) and (3) (Section 2), but the other equations were just guesswork. No one has measured how local velocities vary over time in natural images, as necessary to develop a good Eq. (2). In turn, the Eq. (4) guess is reasonable, as it implies that the mechanism is maximally informative about local speeds. However, the brain may implant other loss functions for speed measurement. For example, it may penalize errors in large speeds more than in low speeds, since the former can occur when a nearby object is approaching dangerously fast.

That the Kalman-adaptation model makes good qualitative predictions suggest that one of the two temporal phases in the slow-to-fast condition corresponds to trusting the past while the other correspondsto trusting the measurements (Section 2). Is the physiological mechanism mediating the slow, past-trusting phase different from that mediating the fast, measurement-trusting phase? If these mechanisms were different, then one mechanism would probably be a hyperpolarization caused by the decrease in the excitation received by a cell (Carandini & Ferster, 1997). Unfortunately, the other mechanism, if existent, is not yet known. Nevertheless, we have an argument against two clearly resolved separate mechanisms. With noise, the slow-tofast condition yields a single time constant that is intermediate between the two time constants without noise. This suggests that a nonlinear dynamic network controls the time course of adaptation, changing the apparent time constants in a stimulus-dependent manner.

Acknowledgments

The work was supported by ANPCyT Grants PICT03-11687 and PICT13-15190 (Argentina) to J.B. and by National Eye Institute Grants EY08921 and EY11170, and ONR Grant N00014-06-1-0746 to N.M.G.

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