REVIEW

Adaptive optimization of visual sensitivity[1]

Sergei Gepshtein* **and Thomas D. Albright***

Center for Neurobiology of Vision
The Salk Institute for Biological Studies
10010 North Torrey Pines Road
La Jolla, CA 92037, USA

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ABSTRACT

Sensory systems adapt to environmental change. It has been argued that adaptation should have the effect of optimizing sensitivity to the new environment. Here we consider a framework in which this premise is made concrete using an economic normative theory of visual motion perception. In this framework, visual systems adapt to the environment by reallocating their limited neural resources. The allocation is optimal when uncertainties about different aspects of stimulation are balanced. This theory makes predictions about visual sensitivity as a function of environmental statistics. Adaptive optimization of the visual system should be manifested as a change in sensitivity for an observer and for the underlying motion-sensitive neurons. We review evidence supporting these predictions and examine effects of adaptation on the neuronal representation of visual motion.

KEYWORDS

VISUAL PERCEPTION, MOTION PERCEPTION, SENSORY ADAPTATION, CONTRAST THRESHOLD, NEURON, RECEPTIVE FIELD, NORMATIVE THEORY, NEURAL ECONOMY, SYNAPTIC WEIGHT, PLASTICITY, SWARM INTELLIGENCE

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* Correspondence should be addressed to either author at *sergei@salk.edu* or *tom@salk.edu*.

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1. *Introduction*

One of the fundamental tenets of sensory biology is that sensory systems adapt to environmental change. It has been argued that adaptation should have the effect of optimizing SENSITIVITY to the new environment. Attempts to corroborate this view in visual neuroscience led to controversy. This is because adaptation to a visual environment has been expected to improve visual performance in that environment, relative to performance before adaptation. This expectation has been contradicted by the fact that adaptation has been observed to have different effects: it can decrease visual performance for the adapting stimulus, or it can leave performance intact, or it can change performance for stimuli very different from the adapting ones.

We proposed that the previous results can be explained by taking an economic perspective on neural function. According to this view, visual adaptation is mediated by reallocation of limited neural resources over a broad range of visual stimulation, i.e., by changing the tuning of multiple NEURONS in the visual cortex. The reallocation is expected to cause gains and losses of sensitivity by neurons tuned to different stimuli. Using a normative theory of neural resource allocation, we predicted that sensitivity changes should form a lawful pattern of gains and losses of sensitivity.

We have tested these hypotheses behaviorally using new PSYCHOPHYSICAL methods that allowed us to assay sensitivity rapidly across a wide range of spatiotemporal stimuli. Statistics of stimuli were varied such that different speeds were prevalent on different days of the experiment. We found that the change of stimulus statistics caused a large-scale reorganization of sensitivity: an orderly pattern similar to that predicted by the theory of adaptive reallocation of neural resources.

The economic theory predicts that the expected change of sensitivity for individual neurons depends on where their tuning falls on the behavioral sensitivity function. We consider the possibility that such changes can be implemented in multiple neurons by means of mutually independent stochastic adjustments of synaptic weights. This mechanisms will require no coordination between the changes in neurons tuned to very different stimuli, similar to the self-organizing process of "swarm intelligence" found in many biological systems.

SENSITIVITY is a measure of how well an organism or a single neuron can detect a stimulus or discriminate between stimuli. Low sensitivity means that the stimulus needs to have a high intensity or high contrast to be detected or to be discriminated from another stimulus. Conversely, high sensitivity means that a low intensity or low contrast of the stimulus is sufficient for its detection or discrimination.

NEURONS are the major cell type in the brain involved in neuronal communication and computation. Signals are communicated electrically *within a neuron* via progressive changes in the voltage difference between the inside and outside of the cell. Signals are communicated chemically *between neurons* via the release of neurotransmitters into the synaptic cleft (the microscopic space between neurons), which in turn activate receptors on the next neuron in the sequence. There are approximately one hundred billion neurons in the human brain.

PSYCHOPHYSICS is the scientific study of the relationship between physical and mental phenomena. Sensory psychophysics concerns the relationship between the physical patterns (called "stimuli") that activate the observer's neural system, on the one hand, and the sensations elicited by the stimuli, on the other hand.

2. *The puzzle of visual adaptation*

2.1 *Adaptation*

Visual adaptation is one of the most striking and well-studied of visual phenomena (Mather et al., 1998). Yet the mechanisms underlying adaptation remain elusive and the evidence for it controversial. Until recently, adaptation was viewed as a manifestation of neural fatigue. The contemporary view is more pragmatic; it holds that adaptation is a response of the organism to changes in statistics of stimulation (e.g., Sakitt & Barlow, 1982). Adaptation is taken to manifest an optimization of the organism's perceptual abilities under changing stimulation. But evidence supporting this view is scarce and inconsistent. For example, some studies of adaptation to moving patterns have shown that speed discrimination performance improves for speeds similar to the adapting speed, but other studies have reported the opposite. Even more surprising are systematic changes in discrimination for stimuli that differ from the adapting. Previous theoretical efforts have failed to provide a comprehensive explanation for these findings.

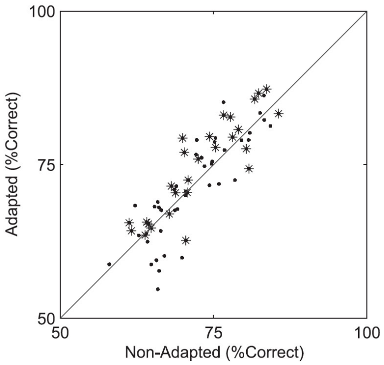

Figure 1: Speed adaptation in cortical area MT (Krekelberg et al., 2006) Neuronal speed discriminability before (abscissa) and after (ordinate) adaptation. Asterisks indicate neurons for which adaptation was significant. The symbols (points and asterisks) above and below the diagonal represent neurons whose discriminability was respectively improved or impaired by adaptation.

Inconsistency is also a property of data obtained in NEUROPHYSIOLOGICAL studies of speed adaptation. Consider, for example, the study of neurons in cortical visual area MT following a brief motion adaptation by Krekelberg et al. (2006). Their main result is summarized in Fig 1. Adaptation was found to reduce firing rates and to alter speed discriminability. These effects were puzzling in two ways. First, the effect of adaptation on response rate reduction was often greatest when the adapting speed was different from the preferred speed of the cell. Second, only some cells showed improved speed discriminability, while discriminability by many other cells was impaired.

NEUROPHYSIOLOGY is the scientific study of the normal mechanisms of neural systems. Neurophysiological studies of visual systems reveal the types of signals carried by neurons and the manner in which those signals are transformed in service of specific visual tasks, such as detection and discrimination of optical signals. It is useful to distinguish neurophysiology from neuroanatomy. The latter is the study of the structure of neural system, made possible by methods for selective visual labeling of brain tissue. The labeling provides a picture of neurons as well as a picture of the wiring diagram of neuronal connectivity.

In the following we describe an attempt to solve the puzzle of motion adaptation from the perspective of neural economy. We consider one of the most studied forms of motion adaptation, quantified in terms of visual contrast sensitivity.

2.2 *Contrast sensitivity*

There are many ways to quantify visual sensitivity (e.g., Robson, 1966, 1993; Nakayama, 1985; Watson & Ahumada, 2016). Perhaps the most comprehensive and systematic of these methods is the one developed by Kelly (1979), illustrated in Fig 2A. Sensitivity in this case reflects CONTRAST THRESHOLD for pattern detection as a function of spatial and temporal frequencies of stimuli, (sf,tf).

CONTRAST THRESHOLD. Stimulus contrast is the difference in luminance or color between the least intensive and most intensive parts of the stimulus. (See "Psychophysics" on page 3 for definition of "stimulus.") Contrast threshold is the lowest value of stimulus contrast that elicits a sensation.

We will describe a theoretical approach to understanding the

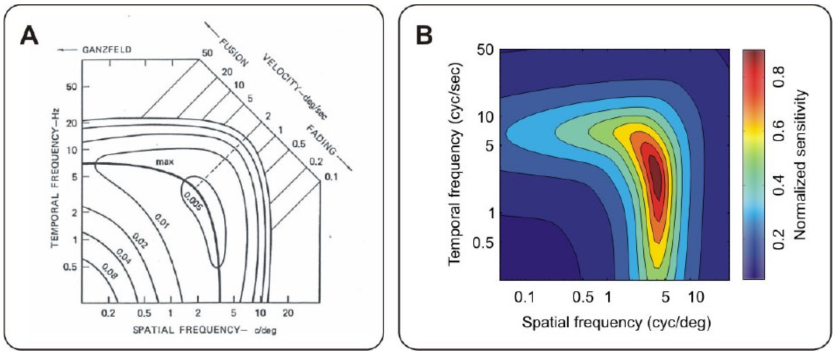

Figure 2: Spatiotemporal sensitivity functions. (A) Plot of luminance contrast thresholds as a function of (sf,tf) (Kelly, 1979b). The heavy line represents maximal sensitivity at every speed, and the contours represent equal increments of log sensitivity. (B) Simulation of (sf,tf) sensitivity for speed discrimination, from principles developed in our theoretical approach (section Innovation). Our preliminary measurements, using intensive psychophysical methods, have yielded a sensitivity function similar to that obtained by Kelly, but with a greatly reduced data collection.

forces that shape the distribution of visual sensitivity across stimuli (Fig 2A). From this perspective it follows that the distribution of visual sensitivity, as well as diverse and seemingly inconsistent transformations of sensitivity induced by adaptation, are manifestations of efficient visual behavior. That is, adaptive changes reflect optimization of visual performance with limited resources. We will then show how this perspective entails specific predictions for the distribution of visual sensitivity, i.e., how visual sensitivity should change in response to changes in stimulation. The changes should form a characteristic pattern across stimuli, including the previously observed results as special cases. In particular, visual sensitivity should either increase or decrease at the prevailing speed of stimulation, depending upon the conditions of measurement. Also, the changes in sensitivity should propagate, in a lawful manner, across the entire stimulus space, including stimuli very different from the adapting ones, as we explain next.

3. *Visual adaptation from a normative perspective*

3.1 Neural economics

We present the economical approach using the plot introduced in Fig 2A. Different points in the plot represent tuning parameters of motion-sensitive neurons (Albright, 1984) at the peak of their sensitivity. The parallel lines are constant-speed lines ("speed lines"). Each such line comprises points at which the ratio of temporal frequency to spatial frequency (i.e., the speed) of stimulus is constant. Low speeds appear at bottom right of the plot and high speeds at top left.

Gepshtein et al. (2007) developed a normative theory of motion estimation that allowed them to derive optimal conditions for estimating every speed. Under these conditions, the uncertainties as-

Spatial and temporal frequencies of stimuli. Spatial frequency is a characteristic of optical stimuli that are periodic across space. It is a measure of how often components of the stimulus repeat per unit of distance. In vision science, the unit of spatial frequency is spatial cycle per degree of visual angle (written as "c/deg" or "cyc/deg"). Similarly, temporal frequency is a characteristic of optical stimuli that are periodic across time. The unit of temporal frequency is Hz, which is temporal cycle per second.

Normative theory. A theory is normative when it specifies optimal performance of a system in view of system limitations (constraints). "Normative" is often contrasted with "descriptive." A theory is descriptive when it specifies the actual performance of the system.

sociated with measurements of different stimuli are balanced.[2] Each optimal condition is represented by a point on the corresponding speed line. Such points for all speeds collectively form an "optimal set," represented in Fig 3 by the red curve. According to this normative theory, the optimal set has the invariant form of a rectangular hyperbola.

From the theory it also follows that the location of the optimal set in the (sf,tf) parameter space depends on the statistics of stimulus speed (Fig 4). For example, suppose that in the natural environment the prevailing speed is low (Weiss et al., 2002), indicated in Fig 4A by the oblique red line. Then suppose that the environment changed and the prevailing speed has increased (oblique green line). The conditions at which the system has greatest sensitivity (the optimal set) is predicted to change, which can be summarized as a shift (a translation) of the optimal set in the (sf,tf) parameters space, as follows.

In Fig 4A, the directions of displacement of optimal points along two speed lines are shown by arrows. For the two indicated speeds, the optimal points are predicted to shift in opposite directions: toward lower spatiotemporal frequencies at the low speed, and toward higher frequencies at the high speed. Thus, whether sensitivity grows or decays at a given location depends on whether the optimal point moves toward or away from that location. There also exist conditions where sensitivity is expected to remain unchanged, e.g., where the new and old optimal sets intersect and the optimal point does not move.

This illustration makes it clear that an adaptation experiment can lead to qualitatively different outcomes depending on the conditions at which motion sensitivity is measured, as shown in Fig 4B. Sensitivity may increase (points 1 & 6), decrease (2 & 5), or not change at all (3 & 4). Paradoxically, it is predicted that sensitivity changes that make the system behave optimally as a whole can lead to sensitivity losses at the currently prevailing speed (point 2). Notice also that

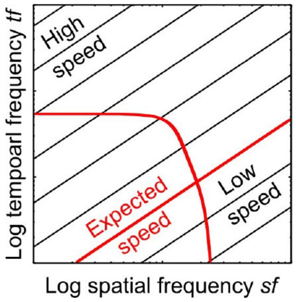

Figure 3: Optimal sets for speed estimation. Oblique lines correspond to different speeds ("speed lines"); they are parallel to one another in the logarithmic coordinates. Speed (v=tf/sf) grows from bottom right to top left of plot. Points predicted to be most suitable for estimation of every speed form a set represented by red curve: the optimal set of speed estimation. According to Gepshtein et al. (2007) the optimal set has an invariant shape, approximated by a rectangular hyperbola. Position of optimal set in the plot depends on prevailing speed of stimulation: the "expected speed" (Fig 4).

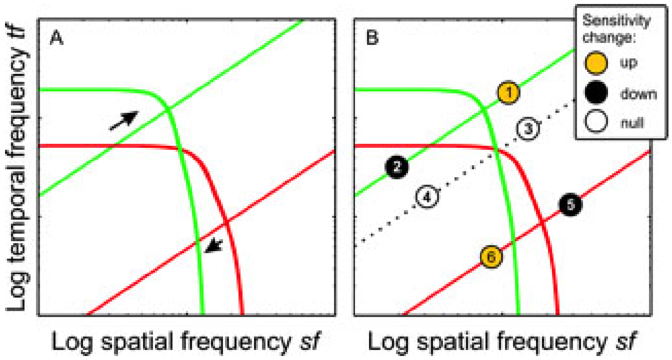

Figure 4: Predicted effects of speed adaptation for optimal conditions. (A) Changes in statistics of stimulation lead to displacement of optimal set for speed estimation: from red curve (low-speed context) to green curve (high-speed context). (B) In effect, different sensitivity changes are expected across the parameter space. Numbered disks mark locations of qualitatively different consequences of adaptation.

[2] These uncertainties concern location and frequency content of stimuli, defined according to the information theory of Gabor (1946), detailed in Gepshtein et al. (2007).

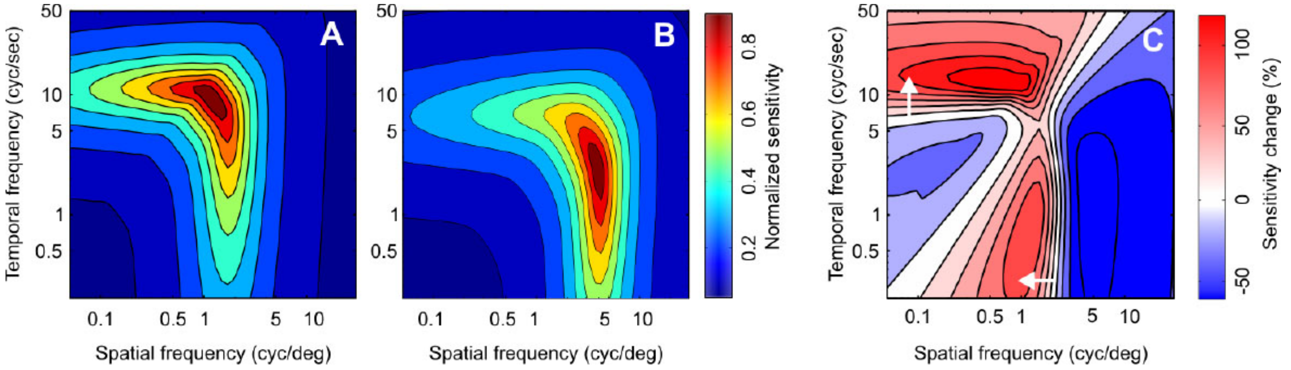

Figure 5: Predicted effect of adaptation for the entire parameter space. (A-B) Predicted distributions of sensitivity in stimulus environments with high (A) and low (B) prevailing speeds. In both panels, warm colors indicate high sensitivity and cool colors indicate low sensitivity (normalized for this figure). (C) Predicted change map. Entries in C are 100*(B-A)/A, where A and B are entries in sensitivity maps of panels A and B. Here, shades of red indicate gains of sensitivity and shades of blue indicate losses of sensitivity

optimization can lead to large sensitivity changes (gains and losses) far away from the prevailing conditions (points 5 & 6). It is expected that the shift of the optimal set is accompanied by sensitivity changes over the entire parameter space, as shown in Fig 5. Figs 5A-B are theoretical distributions of sensitivity in, respectively, high-speed and low-speed environments. Fig 5C is a map of sensitivity change: the shades of red and blue indicate stimulus conditions where sensitivity is expected to increase and decrease.

It is convenient to think of the predicted gains and losses of sensitivity as foci of change formed around branches of the optimal set. Recall that this set resembles a rectangular hyperbola (similar to the curve "max" in Fig 2A). Shifts of this hyperbola create systematic changes across the (sf,tf) plot summarized in Fig 5. This hypothesis is supported by the experiments described in Section 4.

3.2 *The theoretical context*

Theories of perception based on the statistical decision theory, including Bayesian theories, (Knill & Richards, 1996; Simoncelli & Olshausen, 2001; Maloney, 2002) also predict that stimulus statistics affect perception. Here, probabilities of sensory estimates (likelihood functions) and the probabilities of corresponding parameters in the stimulation (prior distributions) are combined by point-by-point multiplication, following the Bayes' rule, making the prevalent stimuli more likely to be seen than the less common stimuli.

To illustrate differences of our approach from the above framework, consider a study of motion adaptation by Stocker & Simoncelli (2006). As it is common in the Bayesian framework, the authors represented effects of adaptation by changes in the prior distribution. The model predicted that adaptation would cause increased similarity ("attraction") of stimuli to the adaptor. Experimental results showed the opposite: a reduced similarly ("repulsion") of stimuli to the adaptor (e.g., Barlow, 1990). To remedy the discrepancy, the authors modeled adaptation by adjusting the likelihood function, rather than the prior distribution. They proposed that "adaptation acts to allocate more resources to the representation of the parameter values in the vicinity of the adaptor ... resulting in a local increase in the signal-to-noise ratio" thus broadening the likelihood function because the resources are withdrawn from conditions removed from the adaptor. Repulsion is caused by the broadening of the likelihood function. The authors had to step outside of the standard Bayesian framework and make an assumption for which they had no principled theory. We would like to contrast their approach with the normative approach presented here, which offers an explicit principled theory that predicts just how a visual system should reallocate its resources in response to changes in stimulus statistics.

4. Adaptive transformation of sensitivity

The formulation of spatiotemporal sensitivity by Kelly (introduced in Fig 2) reflects contrast thresholds for pattern detection as a function of (sf,tf). Nakayama (1985) reviewed multiple other formulations and concluded that "seemingly very different phenomena: [motion aftereffect], pattern detection and direction discrimination, fit a similar set of functions." In other words, the data represented as sensitivity over (sf,tf) all have the general "bent-loaf" appearance reported by Kelly. We chose to assess spatiotemporal contrast sensitivity using a direction discrimination task because it helped to avoid the response biases characteristic of detection tasks.

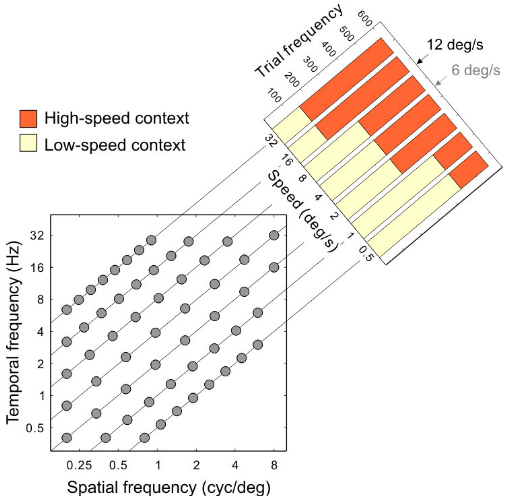

Figure 6: Stimulus grid and statistics for adaptation experiments. Disks represent stimulus conditions arranged on seven constant-speed lines in domain of spatiotemporal sensitivity function (the "stimulus space"). Two complementary histograms at top right illustrate "stimulus contexts." In low-speed context, low speeds are sampled more often. In high-speed context, high speeds are sampled more often. Mean speeds of contexts are 6 and 12 deg/s.

To study how stimulus statistics affect the distribution of contrast sensitivity, we created two stimulus contexts as shown in Fig 6. We varied how often stimuli were sampled from the same stimulus grid, creating two contexts: low-speed and high-speed. We deployed a "quick" method for assessing the Contrast Sensitivity Functions (quick CSF or qCSF) developed by Lesmes et al. (2010; also see Lesmes et al., 2009; Pawar et al., 2013) by generalizing previous procedures for rapid estimation of sensory performance (PSI method by Kontesvich & Tyler, 1999; also Cobo-Lewis, 1997; Kujala & Lukka, 2006).

Examples of sensitivity functions obtained this way are displayed in Fig 7A. Sensitivity changes are plotted (for one subject) in Fig 7B: for two speeds at top and for the entire domain of the sensitivity function at bottom. As in theoretical change map (Fig 5B), sensitivity changes were $d_i = 100(h_i - l_i)/h_i$, where hi and li are respective entries in the high-speed and low-speed sensitivity function. (Change maps for all subjects appear in Fig S2 in Gepshtein et al., 2013.)

The plots in the upper part of Fig 7B demonstrate a reversal of sensitivity change across speeds, as predicted by our theory (Figs 4–5). At the low speed, sensitivity decreased for low frequency conditions and increased for high frequency conditions. At the high speed, the pattern was reversed. The seemingly erratic alterations of sensitivity within the narrow samples of stimulus conditions corroborate the notion that changes of sensitivity must be studied over large stimulus sets.

We evaluated patterns of sensitivity change across full range of (sf,tf) using templates of sensitivity change. The templates consisted of regions where gains and losses of sensitivity were predicted by the theory. We also compared the observed patterns of change to predictions of an alternative theory in which changes of sensitivity merely mirrored changes in stimulation. This analysis overwhelmingly supported our predictions, described in detail in Gepshtein et al. (2013).

5. *Neural mechanisms of adaptation*

5.1 *Approach*

Our analysis of factors that control contrast sensitivity and the results of our psychophysical experiments (Gepshtein et al., 2013) demonstrate that local changes of sensitivity appear paradoxical when viewed in isolation but make sense in a larger context. These discoveries lead us to ask how multiple local changes are coordinated across the vast domain of visual sensitivity. Do visual systems monitor the distribution of stimuli? Is there a mechanism dedicated to

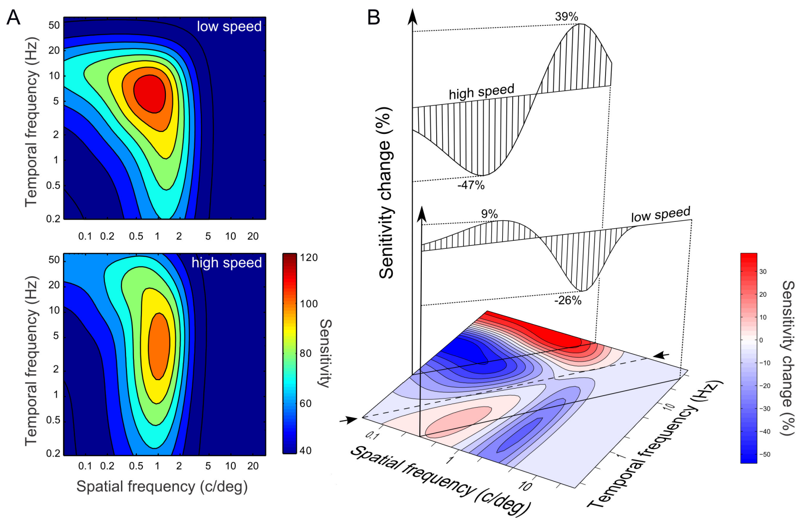

Figure 7: Results of a large-scale assay of sensitivity change. (A) Contrast sensitivity functions measured in two stimulus contexts for one S. Standard model of contrast sensitivity (Kelly function) was fitted to estimates of sensitivity in high-speed (top) and low-speed (bottom) contexts. Warm and cool colors represent high and low sensitivities. (B) Change map at bottom summarizes how sensitivity changed from the low-speed to high-speed stimulus contexts. Shades of red and blue represent gains and losses of sensitivity; white regions represent no change. At top samples of sensitivity changes for two speeds demonstrate that pattern of gains and losses of sensitivity is reversed across speeds, similar to prediction shown in Fig 5.

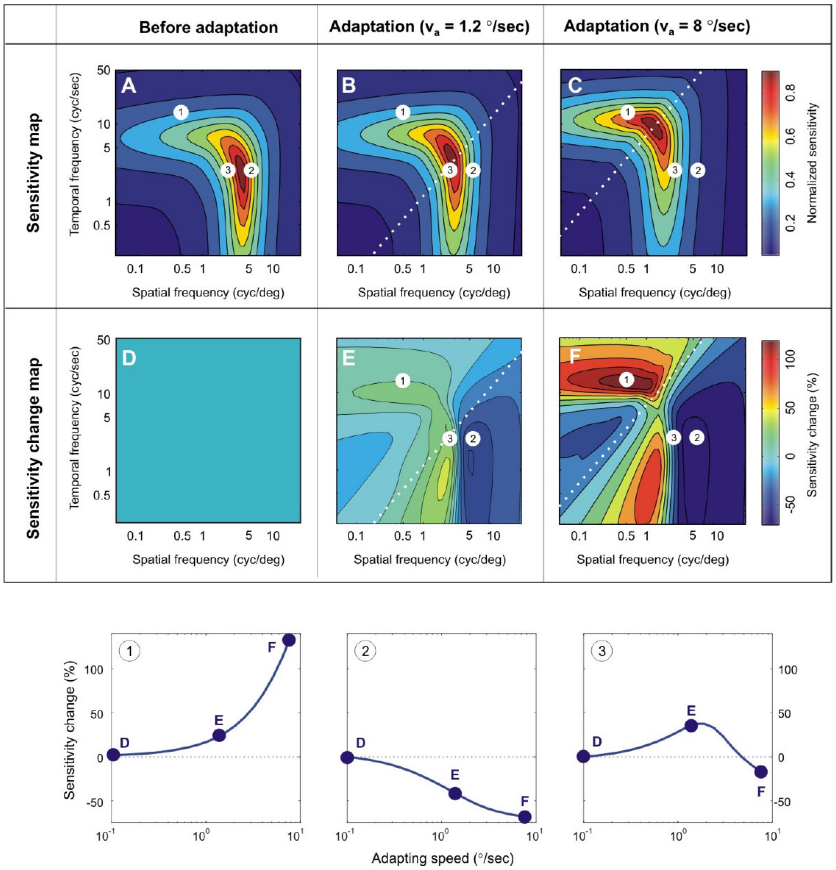

Figure 8: Predicted effects of speed adaptation on sensitivities of individual cortical neurons. Top row of panels illustrate global (sf,tf) "sensitivity maps." (A) Pre-adaptation state depends upon distribution of speeds in the natural world (Dong & Atick, 1995). (B) Expected sensitivity following adaptation to 1.2°/sec (speed indicated by diagonal line). (C) Sensitivity following 8°/sec. As adaptation speed increases, global pattern of sensitivity retains "bent loaf" shape but shifts markedly. Middle row of panels (D, E, F) illustrate fractional change in global sensitivity at indicated speeds (in D, change is nil, by definition). In panels A-F we have indicated preferred (sf,tf) values for three hypothetical MT neurons. Predicted changes in neuronal sensitivity as a function of adapting speed are summarized for each of the three neurons in panels 1-3, at bottom. See text for further detail.

coordinating the distribution of sensitivity?

Our general prediction is that responses of individual neurons (assessed as in Thiele et al., 2000) will reflect changes of sensitivity discovered using psychophysical methods. Because the operating range of the (sf,tf) function for a given neuron will generally cover only a small portion of the behavioral (sf,tf) range, the predicted changes of the neuronal CSF are likely to be evident by one or both of: (1) the overall gain of the neuronal spatiotemporal frequency tuning function may either increase or decrease, (2) the peak of the neuronal (sf,tf) sensitivity function may shift. The study by Krekelberg et al. (2006) summarized in Fig 1 provided preliminary evidence for both of these neuronal effects.

The general nature of predicted changes is illustrated in Fig 8. Panel A portrays the global sensitivity function predicted for a low prevailing speed of $0.1°/s$. Suppose that we record three MT neurons whose peak (sf,tf) preferences lie at the locations indicated by nodes ①, ②, and ③. Neurons ② and ③ lie near the peak of sensitivity, while neuron ① lies at a point of low sensitivity. Global effects of adaptation on sensitivity are illustrated in panel B: The sensitivity function has shifted slightly relative to its position in panel A. Panel E illustrates change in sensitivity from A to B. Neuron ② is expected to undergo a decline in sensitivity, while neurons ① and ③ are expected to become more sensitive.

Similarly, panel C portrays the sensitivity function predicted for the prevailing speed of $8°/s$, and panel F portrays the corresponding change in sensitivity. Sensitivities of the three neurons change: a marked increase for neuron ①, a substantial loss for neuron ②, and little change for neuron ③.

Predicted sensitivity changes for these neurons are summarized at bottom of Fig 8. The horizontal axis in each figure indicates the prevailing speed; the vertical axis indicates sensitivity change. These simulations lead to the provocative prediction that sensitivity of individual neurons should change as a function of adaptation following a highly principled rule, in which the sensitivity change for a given neuron depends upon its position relative to the behavioral sensitivity change map. The second possibility (hinted at by results of Krekelberg et al., 2006) is that psychophysical changes of sensitivity will be correlated with shifts of neuronal preference (not shown).

To understand the factors that control the distribution of neuronal sensitivities we investigated how basic mechanisms of synaptic plasticity in single cells respond to changes of stimulation within their RECEPTIVE FIELDS (RFs). We pursued two specific goals: first, to characterize local changes of sensitivity and, second, to investigate the global distribution of these changes across the entire stimulus domain. Next we describe numerical simulations of synaptic plasticity in SPIKING neural networks performed by in pursuit of both goals (Jurica et al., 2013; Gepshtein, 2014).

RECEPTIVE FIELD is the part of sensory space that, when stimulated, leads to a change in the activity of a sensory neuron (a neuronal response). In the case of vision, the receptive field of a neuron is defined by the region of visual space that, when stimulated, activates the neuron, and by the sensory attributes of the activating stimulus, such as its spatial or temporal frequency (see the previous entry) or direction of motion.

SPIKING. A brief stereotyped neuronal signal is called formally an "action potential" and informally a "spike." An action potential typically sweeps from the cell body along the length of the output process (axon) of a neuron. This neuronal signal results from a rapid, active, and propagating exchange of ions across the cell membrane. Neuronal communication is mediated, in part, by the frequency of action potentials (the frequency of neuronal "spiking"). Simulations of neuronal activity in artificial neural networks are more realistic when they represent neuronal activity in terms of spiking, i.e., using the so-called "spiking neural networks."

5.2 Basic neural circuit

Fig 9A is a diagram of the generic circuit used in simulations of synaptic plasticity. The circuit consists of one readout cell R and two input cells I_1 and I_2. Input cells have receptive fields of different sizes on a single dimension x.[3] The receptive field size of I_2 is larger than that of I_1.

The receptive field size of the readout cell (S_r) depends on the synaptic weights (w_1 and w_2), which determine which of the input cells has a larger effect on R. For example, when $w_2 > w_1$, the size S_r is similar to the size of I_2 (i.e., is larger than in the cases when $w_1 = w_2$ or $w_1 > w2$). Substantial changes in the weights w_1 and w_2 will entail changes in the receptive field size of R.

The weights w_1 and w_2 depend on the relative timing of presy-

[3] This dimension could be space or time. For example, when x represents space, the larger number of lower-level cells (from which the cell I receive information) corresponds to a larger receptive field size of I.

naptic and postsynaptic spiking (Bienenstock et al., 1982; Paulsen & Sejnowski, 2000; Bi & Poo, 2001). When one of the input cells (presynaptic) and the readout cell (postsynaptic) co-fire, the corresponding weight increases. For example, when the cells I_2 and R co-fire more often than the cells I_1 and R, the weight w_2 increases more often than the weight w_1. In that case, the receptive field size of R becomes larger, i.e., more similar to the size of I_2 than I_1.

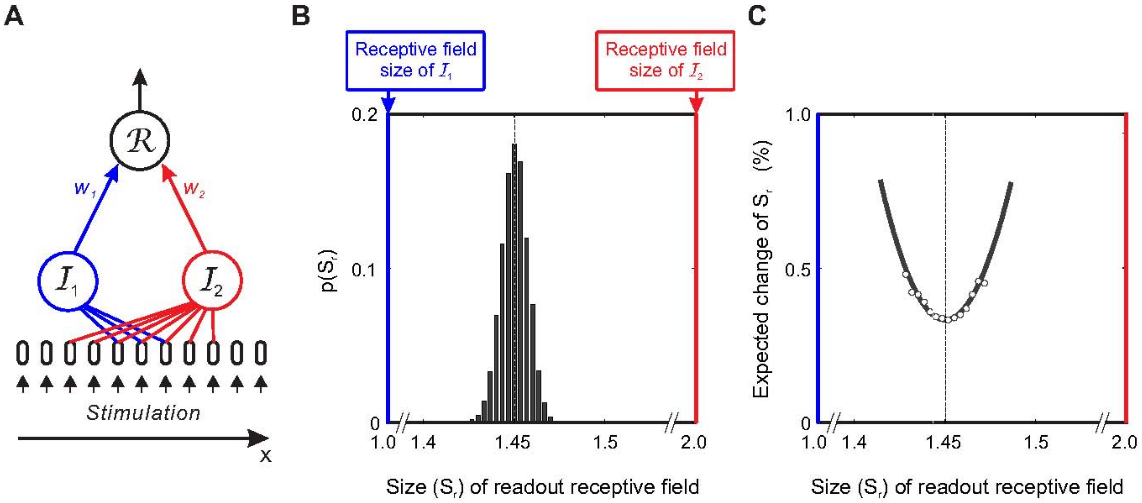

Figure 9: Generic neural circuit. (A) Circuit consists of two input cells (I_1 and I_2) and one readout cell R. The receptive field (RF) size of I_1 is smaller than of I_2 (represented by the number of lower-level cells from which it receives information: three such cells for I_1 and seven for I_2). The RF size of readout cell (S_r) depends on weights w_1 and w_2. (B) The weights are updated according to the stochastic co-activation of input and readout cells. Readout RF size S_r fluctuates on the interval between the sizes of input cells (here normalized to 1 and 2). The histogram of S_r reveals the central tendency of the fluctuation. $p(S_r)$ is the probability of S_r. (C) Small circles represent average changes of S_r (i.e., the amplitude of RF size fluctuation) for different magnitudes of S_r. The farther S_r is from its central tendency the larger the amplitude.

5.3 Receptive field dynamics

Because neuronal firing is a stochastic process, updating of synaptic weights is also a stochastic process that leads to temporal fluctuations of readout RF size. In Fig 9B-C we illustrate two important features of these dynamics. First is the central tendency of readout RF size. The fluctuations of readout RF size are confined to the interval between the smallest (blue) and largest (red) input RF sizes. Probabilities of readout RF sizes over the course of one simulation are captured in the histogram in Fig 9B (see Jurica et al., 2013 for details). The peak of the histogram in Fig 9B corresponds to the most likely readout RF size (S_r^*): the central tendency of readout RF fluctuation.

The second important feature of readout dynamics is the *amplitude of fluctuations* (Fig 9C). The amplitude is low when the readout RF size is similar to S_r^* and it is larger when readout RF size is removed from S_r^*. We illustrate the consequences of these dynamics in Figs 10-11.

Our numerical simulations of synaptic plasticity revealed that fluctuations of RFs are biased by stimulation. The dynamics are best described as drift of the readout RF in (sf,tf) space, where drift direction is determined by local stimulus statistics. In Fig 10, we illustrate this drift in a circuit of 25 input cells and one readout cell.

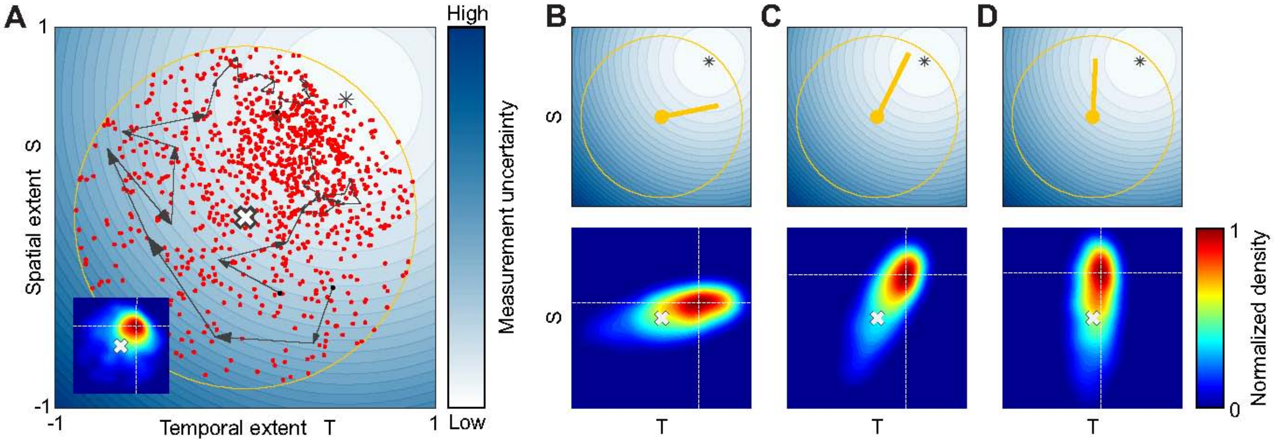

Figure 10: Stochastic tuning of one receptive field. (A) Outcomes of 1,000 simulations for one readout cell and 25 input cells. The two dimensions represent spatial and temporal sized of receptive fields (RF) normalized so that the initial RF size of the readout cell corresponds to (0, 0) marked by the white cross. In each simulation, input-readout weights were updated 700 times. Final parameters of each readout RF are represented by a red dot ("endpoint"). Twenty steps for three of these simulations are illustrated by the gray-arrow trajectories. The contour plot in the background is the average amplitude of fluctuation: a two-dimensional generalization of the curve in Fig 9C. The inset in A is a histogram of endpoint density plotted as a heat map: the warmer the color the higher endpoint density. The central tendency of fluctuation (the peak of endpoint density) is marked by the intersection of while gridlines in the inset and by the asterisk in the main plot. (B-D) Stimulus bias. Mean speeds of stimuli were low in B, intermediate in C, and high in C. The bottom histograms depict endpoint density (as in the inset of A). They show that outcomes of RF fluctuation are biased by the stimulation. The directed yellow markers in top panels point in the direction of RF drift: from the initial condition (central disk) to mean endpoint. These markers are used in Fig 11 to summarize drift of readout RFs across (sf,tf) space.

First consider panel A, where the stimulation was uniform. The central white cross identifies the initial parameters of the readout RF for every simulation. Each red point corresponds to the readout RF parameters after one of 1,000 simulations. The distribution of endpoints (summarized in the inset) is an outcome of correlation between the amplitude of RF fluctuation and the proximity of RF parameters to the central tendency of fluctuation.

Stimulus statistics change the central tendency of fluctuation and thus bias the direction of RF drift. Results in Fig 10B-D were obtained under different stimulus statistics, biased towards low (B), intermediate (C), or high (D) speeds. Direction of RF drift is different in these cases, represented by the directed markers on top of panels B-D.

Notice that stimulus dimension x in Fig 9A could stand for either location or frequency content of the stimulus. We introduced the circuit in terms of RF size (i.e., assuming x was location), to help intuition and to follow Jurica et al. (2013). The two-dimensional generalization in Fig 10 followed the same convention. In what follows we present results of our simulations of RF plasticity in the frequency domain because our present stimuli are defined by frequencies of luminance modulation and because we study effects of adaptation on contrast sensitivity, which is traditionally rendered in the frequency domain.

In Fig 11 we summarize RF dynamics for multiple locations in (sf,tf) space. The simulations were performed as in Fig 10, except the parameters of input RFs and the stimuli were selected according to the location in the (sf,tf) space, as described in Jurica et aI. (2013). The initial condition for every simulation is indicated by a point and the direction of RF drift is indicated by a line. The flow pattern in Fig 11 is a result of the different biases of RF fluctuations created by the different stimulus conditions in different parts of the (sf,tf) space.

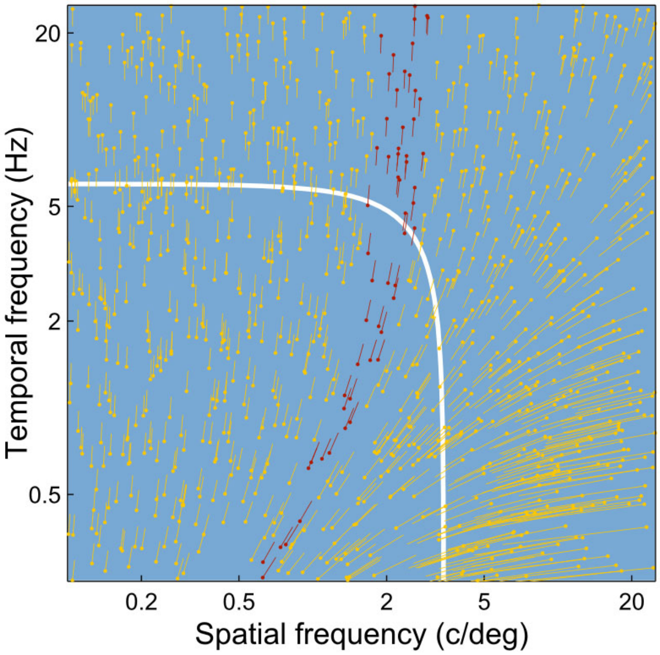

Figure 11: Pattern of receptive field drift across (sf,tf). The same simulations as in Fig 10 were performed at multiple (sf,tf) condition. Local drift directions are represented by the markers introduced in Fig 10B-C. These directions form a systematic global pattern. These results suggest that the globally optimal receptive field allocation predicted by the theory of Gepshtein et al. (2008) can be achieved by local means alone, requiring no mechanism that coordinates the local processes. (The white curve is the sum of conditions on which the local processes converge yielding the highest RF density.)

This analysis predicts that the adaptive changes of individual neurons should follow a regular pattern determined by the local stimulus statistics. When stimulus statistics change, it is expected that the distribution of sensitivity will change too (not shown in Fig 11). We have performed simulations of such changes of neuronal tuning using the same manipulation of stimulus statistics as in our psychophysical experiments (Fig 6). We found that adaptive changes form a global pattern consistent with both the theory of RF allocation (Figs 4-5) and results of our psychophysical experiments (Fig 7) (Gepshtein et al., 2012). Now we pursue a program of studies aimed to test the hypothesis that changes in the population distribution of sensitivities of motion-sensitive neurons in cortical area MT reflect the changes in the distribution of behavioral spatiotemporal sensitivity.

6. Conclusions

The significance of this work is both theoretical and empirical. These studies implement a new way of thinking about sensory adaptation as an economic optimization of the visual system through reallocation of limited neuronal resources. This approach has inspired us to do new kinds of experiments and look at the results of these and other experiments from a new principled perspective. We pointed out that adaptive changes of sensitivity appear paradoxical from a local perspective, i.e., by studying sensitivity in narrow bands of stimulus parameters. The paradox is resolved by taking a broader perspective, i.e., by studying the distribution of sensitivity across a broader range of spatiotemporal conditions.

The broader perspective also points to new questions about the mechanisms of neuronal change. We have described a model of how the synaptic plasticity could implement tuning changes of individual cells. The model suggests that changes should follow a regular pattern: peak sensitivities of cells should follow different paths in different parts of the space of RF parameters, while the directions of these paths should form a gradient across RF parameters (Gepshtein, 2014). We expect that the sensitivity changes of individual cells will form a global pattern consistent with our predictions. Forthcoming studies will show whether this prediction holds.

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Authors

Sergei Gepshtein, Ph.D., is trained in neurobiology, experimental psychology, and vision science. He investigates perceptual experience and behavior from the mechanistic point of view of neuroscience and from a point of view that respects experience as a research focus in its own right. As a member of the Center for Neurobiology of Vision at the Salk Institute for Biological Studies in La Jolla, California, he studies boundaries of perception in the natural world and in sensory media using methods of psychophysics and computational neuroscience. In 2017, he founded the Center for Spatial Perception & Concrete Experience at the University of Southern California in Los Angeles, where basic, translational, and applied studies of perception are combined to create new forms of immersive media.

Thomas D. Albright, Ph.D., is a Professor and Conrad T. Prebys Chair at the Salk Institute for Biological Studies in La Jolla, California. His laboratory seeks to understand the brain bases of visual perception, memory, and visually guided behavior. Albright received a Ph.D. in psychology and neuroscience from Princeton University. He is a member of the US National Academy of Sciences, a fellow of the American Academy of Arts and Sciences, and a fellow of the American Association for the Advancement of Science. Albright is a member of the Scientific Advisory Committee for the Indian National Brain Research Center and was the IISc-DST Centenary Chair Visiting Professor in the IISc Center for Neuroscience from 2011-2013. He is co-organizer of the biennial Bangalore Workshop on Cognitive Neuroscience.