Form 2-4-2

Japan-US Brain Research Cooperative Program
The Group Joint Study Report [field: 4]

1. The Representative of Group Joint Study:
   Affiliation/ Title/ Name
   RIKEN Brain Science Institute, Lab. for Perceptual Dynamics, Researcher,
   Dr. Gepshtein, Sergei

2. The Project Title:
   Making sense of motion adaptation

3. Japanese Investigator's Name, Title, Affiliation and Phone Number:
   Chief: **RIKEN Brain Science Institute, Lab. for Perceptual Dynamics, Researcher,**
   Dr. Gepshtein, Sergei
   Collaborator:

4. U.S. Investigator's Name, Title, and Affiliation:
   Chief:
   Dr. Albright, Thomas D.
   Professor and Director, Vision Center Laboratory, The Salk Institute for Biological Studies
   Collaborator:
   Dr. Lesmes, Louis A.

5. The Term of Research: From Y. 2007 M.4 D. 1 To Y. 2009 M. 3 D. 31 (2 Years)

6. The Abstract, the Result and the Significance of Research(300 Words):

The focus of this work has been on developing and testing a new normative theory of visual sensitivity. A basic premise of our approach is that computational resources of neural systems are limited such that the systems can benefit from allocating more of their resources where they are most useful. We study visual systems where the limited resources are visual neurons or visual receptive fields. We have developed and comprehensively tested a theory that prescribes how the visual resources ought to be distributed across the entire space of parameters of visual stimulation (the "visible spatiotemporal world") such that more resources are allocated where the measurements are more efficient and where the resources are more likely to be used because of the statistics of stimulation. Our results are the first conclusive evidence that visual adaptation is an optimal response of the visual system to changes in the environment. Previous work showed that visual adaptation may sometimes improve sensitivity. But why improvements occur at some adapting conditions and not others, and why the improvements are accompanied by depressions of sensitivity: at the adapting conditions and elsewhere, had remained a mystery. Now we have shown that some depression of sensitivity is inevitable in an optimal visual system with limited resources and that the increments and decrements of sensitivity occur where predicted. Just as perceptual illusions manifest an optimization of sensory systems that accidentally leads to distortions of perception, visual adaptation manifests an overall optimization of visual performance that accidentally leads to depression of sensitivity to some stimulus conditions.

7. The Others (Other Comments):

   Please see the enclosed summary of research (six pages).

Research Report of Collaborative Japan-US project:

Making sense of motion adaptation

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1. Background and Significance

The focus of this work has been on developing and testing a new normative theory of visual sensitivity. A basic premise of our approach is that computational resources of neural systems are limited such that the systems can benefit from allocating more of their resources where they are most useful. We study visual systems where the limited resources are visual neurons or visual receptive fields. We have developed and comprehensively tested a theory that prescribes how the visual resources ought to be distributed across the entire space of parameters of visual stimulation (the "visible spatiotemporal world") such that more resources are allocated where the measurements are more efficient [2, 5] and where the resources are more likely to be used because of the statistics of stimulation [5]. Since the prescribed allocation depends on the statistics of stimulation, we predicted that changes in the statistics must cause systematic and specific changes of visual sensitivity, similar to those observed in studies of *motion adaptation*.

Motion adaptation is one of the best known and most studied instances of neural adaptability. Yet the evidence of motion adaptation has been inconsistent. It has long been expected that adaptation ought to improve visual sensitivity to the prevailing properties of the visual world. But experimental studies found that the sensitivity to adapting stimuli sometimes increases and sometimes decreases, or it does not change at all. Also, large changes of visual sensitivity were found for stimulus conditions very different from the adapting ones. For example, Krekelberg *et al*. [8] observed all these effects in adaptation to speed of visual motion.

From our theoretical perspective, the pattern of sensitivity changes that puzzled researchers of motion adaptation is expected. We have argued that improvements of sensitivity at some stimulus conditions must be accompanied by depressions of sensitivity at some other stimulus conditions, because the overall amount of visual resources is limited.　We predicted that the changes of sensitivity must form a *distinctive pattern* across the space of stimulus conditions. This is because the basic characteristic of visual sensitivity—the spatiotemporal contrast sensitivity function [7]—has a peculiar "bent loaf" shape in that space (Fig 1A). We have shown that this shape is not accidental, but is expected from first principles [5]. We have also shown that the position of the "bent loaf" in the space of parameters must depend on the statistics of stimulation. When the statistics change, the "bent loaf" is predicted to shift to a new location in the space of parameters. For example, if the prevailing speed of stimulation increases, the distribution of sensitivity is expected to shift toward the high speeds in the top left corner of the space of parameters (Fig 1B). Because of this *global shift* of sensitivity, the local changes of sensitivity are expected to vary gradually across the space of parameters, forming foci of positive and negative changes at predicted locations, at the adapting conditions and away from them (Fig 1C).

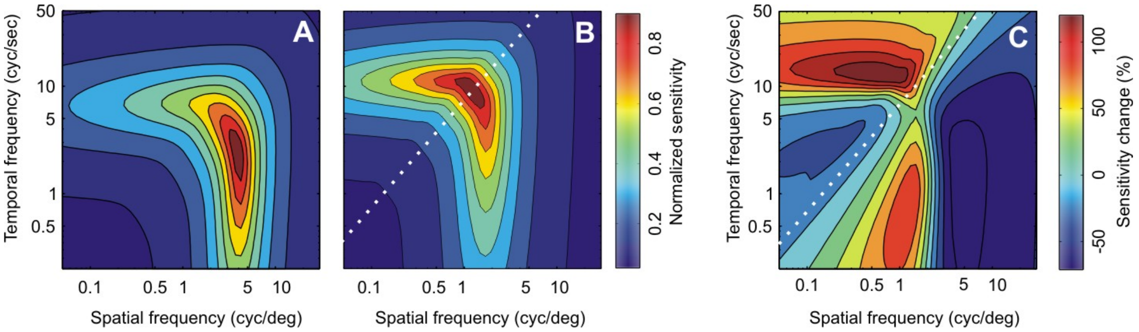


Fig 1: Predicted consequences of motion adaptation across the entire space of spatial and temporal parameters of stimulation. **(A)** The distribution of sensitivity in a system adapted to low speeds. It is the well-known *spatiotemporal contrast sensitivity function* (Kelly, 1979): the "bent loaf." **(B)** In response to an increase in the prevailing speed of stimulation, the distribution of sensitivity is predicted to change such that high sensitivities are moved toward the higher speeds. (The new mean speed is indicated by the dotted diagonal line at 8°/sec.) In **A** and **B**, the warm and cool colors represent, respectively, the high and low sensitivities (see color bar). (**C**) Distribution of predicted *sensitivity changes*. Entries in map **C** are 100*(*B-A)/A*, where *A* and *B* are the entries in the sensitivity maps **A** and **B**, respectively. Here, the warm and cool colors represent, respectively, increased and decreased sensitivity. Note that both positive and negative changes of sensitivity are expected along the dotted line: the mean adapting speed. Also, large changes of sensitivity are expected away from the mean adapting speed.

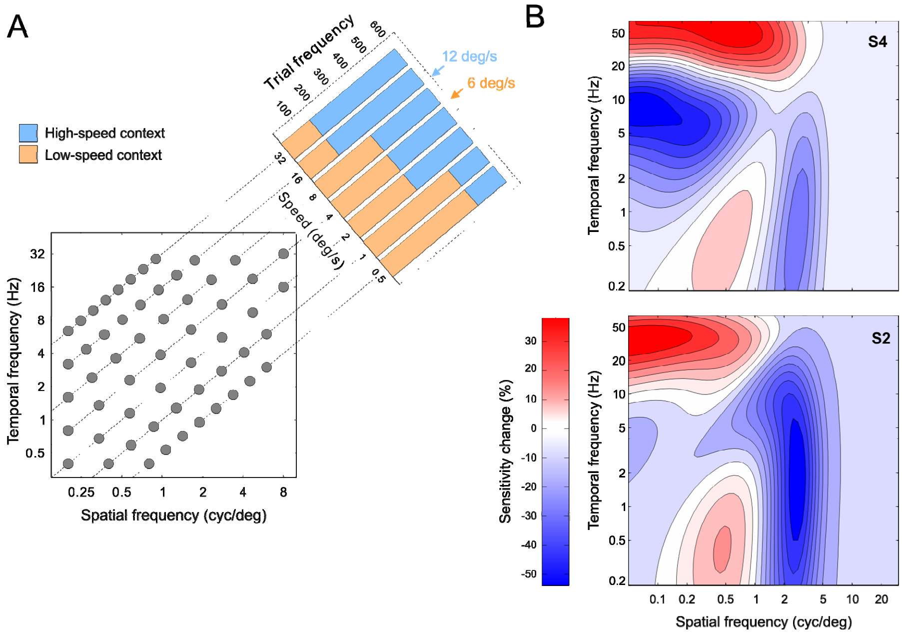
2. Results

2.1. Experimental studies. We have obtained a conclusive confirmation of the predictions described above. We measured human contrast sensitivity over a large span of spatial and temporal frequencies of drifting luminance gratings. Each gray circle in Fig 2A represents one such grating in the space of spatiotemporal parameters, the grid of stimulus parameters selected such as to capture the most informative part of the contrast sensitivity function. The observers viewed the drifting gratings of variable contrast and discriminated the direction of motion. We varied the statistics of speed in our stimuli (Fig 2A): in some blocks of trials low speeds were more common than high speeds ("low-speed context"), and in other blocks of trials high speeds were more common than low speeds ("high-speed context").

We measured large portions of the spatiotemporal contrast sensitivity functions in both contexts using a novel intensive procedure [9-10]. We first ascertained that in every observer the measured sensitivity functions had the same shape as described by Kelly [7]. We then used the equations derived by Kelly to fit our data. Next we compared the sensitivity surfaces obtained in the two contexts. We found that the changes of sensitivity were very similar to the predicted ones (Fig 2B): The changes were global. They formed foci of increased and decreased sensitivity across the space of parameters, forming a pattern similar to the one predicted by the theory (Fig 1C).

These results are the first conclusive evidence that visual adaptation is an optimal response of the visual system to changes in the environment. Previous work showed that visual adaptation may sometimes improve sensitivity (e.g., [1,8]). But why improvements occur at some adapting conditions and not others, and why the improvements are accompanied by depressions of sensitivity: at the adapting conditions and elsewhere, had remained a mystery. Now we have shown that some depression of sensitivity is inevitable in an optimal visual system with limited resources and that the increments and decrements of sensitivity occur where predicted. Just as perceptual illusions manifest an optimization of sensory systems that accidentally leads to distortions of perception, visual adaptation manifests an overall optimization of visual performance that accidentally leads to depression of sensitivity to some stimulus conditions.

Fig 2: Testing the normative predictions. (**A**) Design of experiments. The circles represent the stimulus conditions sampled by the adaptive procedure. The histogram on top right represents stimulus distributions in two types of blocks of trials: In the “high-speed context” high speeds were presented more often than low speeds; in the “low-speed context” low speeds were presented more often. The arrows mark the mean speeds of the two contexts. (**B**-**C**) Change maps in two experimental subjects computed as in Fig 1C. The shades of red and blue represent, respectively, increased and decreased sensitivity (see color bar).



We have reported different aspects of this work as follows:

- Sloan-Swartz Meeting on Theoretical Neuroscience, Princeton University, July 19-22, 2008 (http://brodylab.princeton.edu/SloanSwartz2008/program.html).
- Invited talk *Gabor's Uncertainty Principle in Visual Perception and Adaptation* at the Dept. of Psychology at Rutgers University in New Brunswick (December 11, 2009).
- Invited talk *Gabor's Uncertainty Principle and Vision* at the *Neurotheory Seminar*, Center for Theoretical Neuroscience, Columbia University (December 12, 2009; www.neurotheory.columbia.edu/calendar.html).
- Annual meeting of *COSYNE: Computational and Systems Neuroscience* conference (published as Gepshtein S, Lesmes L, Tyukin I and Albright T. 2009. Sensory adaptation as an optimal redistribution of neural resources. *Frontiers in Systems Neuroscience. Conference Abstract: Computational and systems neuroscience*. doi: 10.3389/conf.neuro.06.2009.03.336).
- Annual meeting of the *Vision Sciences Society* (talk delivered on May 10, 2009; in press in *Journal of Vision*).
- Abstract submitted to the *Society for Neuroscience* annual meeting (Chicago, October 17-21, 2009).

We are preparing three journal articles about this work:

1. about the experimental confirmation of normative predictions and the reconciliation of results in motion adaptation;
2. about the new adaptive methods we developed to measure the sensitivity surface: rapidly and yet comprehensively;
3. a review of our approach for *Trends in Neural Sciences*. (*TINS* have expressed interest in publishing the review.)

Besides testing the predictions of our theory for sensory adaptation, we have been developing other aspects of our approach to sensory systems:

2.2. Theoretical studies. We have formulated a comprehensive mathematical theory of optimal resource allocation in the visual system, beyond the first formulation in [5]. The first publication was geared to the vision science community, which forced us to use the mathematical argument sparingly. Here we aim to present our work in the full mathematical detail, while we publish descriptive and qualitative accounts of our approach separately (the review in *Trends in Neural Sciences* mentioned above).

4. We are preparing a manuscript *A normative-economic approach to motion sensing*, to be submitted to *Neural Computation* in the summer of 2009, in collaboration with Dr. Ivan Tyukin of the Dept. of Mathematics of Leicester University:

> *Abstract*. Theoretical studies of biological motion sensing have often focused on elementary mechanisms of motion measurement called “motion detectors” or “motion sensors.” Our present concern is different. We investigate how motion sensors ought to be allocated across the conditions of spatiotemporal

simulation such that errors in estimating the parameters of motion in the environment are as small as possible. We approach the question from an economic perspective, seeking an optimal allocation of limited system resources: a finite number of motion sensors. We investigate how the prescription of optimal allocation depends on the constraints that are intrinsic and extrinsic to the visual system (such as Gabor's uncertainty principle of measurement and the statistics of stimulation, respectively), and how system performance depends on different kinds of intrinsic and extrinsic noise.

2.3. Design of optimal sensory systems. We have simulated a network of uncoupled neuron-like elements sensitive to visual motion. We have shown that by randomly updating the tuning of elements to parameters of stimulation, while the changes of tuning are proportional to local uncertainty of measurement (as in [2]), the simulated sensory system can steer itself toward the optimal state predicted by our theory and consistent with the empirical measurements of sensitivity in biological vision. This is a demonstration of (a) how the optimal allocation can be implemented mechanistically, and (b) how our normative approach can be used to model the *development of visual sensitivity*. An early report about this work had been published in peer-review proceedings of the International Conference on Intelligent Sensors, Sensor Networks and Information Processing [6].

5. We are now preparing a detailed report about this work for a journal publication, in collaboration with P. Jurica of RIKEN Brain Science Institute, Japan:

Abstract. We propose a design for unsupervised adaptive optimization of sensory systems. We consider a network of sensors that measure stimulus parameters as well as the uncertainties associated with these measurements. No prior assumptions about the stimulation and measurement uncertainties are built into the system, and properties of stimulation are allowed to vary with time. We present two approaches: one is based on estimation of the local gradient of uncertainty, and the other on random adjustment of cell tuning. Either approach steers the network towards its optimal state.

2.4. Physiological experiments*.* We have developed specific predictions for single-sense measurements of neural activity in areas V1 and MT of behaving non-human primates, which we will carry out as soon as we obtain governmental funding dedicated to the physiological studies. We have applied for funding from the

6. The National Institute of Health of the United States of America (application titled "Neural mechanisms underlying adaptive optimization of visual sensitivity"),

7. The National Science Foundation of the United States of America (application titled "Adaptive sensitivity to visual motion: Theoretical principles and neural mechanisms").

The reviews have been positive, but we have not been granted the funding yet. We are now preparing revised applications to both the NIH and NSF.

2.5. Other work. In addition to the above, the funding from the National Institute of Natural Sciences has helped to support the following work:

8. Gepshtein, S. (2009). Closing the gap between ideal and real behavior: Scientific vs. engineering approaches to normativity. *Philosophical Psychology* **22** (1): 61 – 75 (http://philpapers.org/rec/GEPCTG). This article is a nontechnical review of modern normative approaches to sensory and sensorimotor behavior written for the general scientific audience:

Abstract. Early normative studies of human behavior revealed a gap between the norms of practical rationality (what humans ought to do) and the actual human behavior (what they do). It has been suggested that, to close the gap between the descriptive and the normative, one has to revise norms of practical rationality according to the Quinean, engineering view of normativity. On this view, the norms must be designed such that they effectively account for behavior. I review recent studies of human perception which pursued normative modeling and which found good agreement between the normative prescriptions and the actual behavior. I make the case that the goals and methods of this work have been incompatible with those of the engineering approach. I argue that norms of perception and action are observer-independent properties of biological agents; the norms are discovered using methods of natural sciences rather than the norms are designed to fit the observed behavior.

9. Gepshtein, S. Elements of sensation from Fechner and Brentano to Gabor. Manuscript in preparation. This article is an invited contribution to the special issue *Roots of Psychophysics*, to be published an interdisciplinary journal *Philosophical Psychology*:

Abstract. Two traditions have had formative influence on the theoretical and experimental research of perception. One tradition is statistical, stretching from Fechner's enunciation of psychophysics in 1860 to the modern view of perception as statistical decision making. The other tradition is phenomenological: from Brentano's "empirical standpoint" of 1874 to the gestalt movement and the modern work on perceptual organization. Each tradition has at its core a distinctive assumption about indivisible components of perception: the just-noticeable differences in the tradition of Fechner vs. phenomenological "complexes" or gestalts in the tradition of Brentano. But some key results from the two traditions can be explained and connected using an approach that is neither statistical nor phenomenological. The approach rests on a basic property of any measurement: the uncertainty principle formulated by Gabor in 1946 as a part of his quantal theory of information. Here the indivisible components are *units of information* that remain invariant under changes of precision of measurement. This approach helped to understand how sensory measurement are implemented by single neural cells. But recent studies suggested that this approach may be expanded beyond the measurements by single cells and explain large-scale characteristics of sensory systems.

10. Dr. Gepshtein co-edited an exceptionally successful special issue (37 articles) of the *Journal of Vision* titled *Perceptual Organization and Neural Computation* (http://journalofvision.org/8/7/), introduced in: Gepshtein, S., Elder, J. H., & Maloney, L. T. (2008). Perceptual organization and neural computation. *Journal of Vision*, *8*(7), 1-4, http://journalofvision.org/8/7/i/.

11. Dr. Gepshtein is preparing an edited book (with Dr. Laurence Maloney of the New York University) under the tentative title *Oxford Handbook of Perceptual Organization*. The Oxford University Press has expressed its commitment to publish the book in the new *Oxford Library of Brain and Behavior* (Contact: Dr. Catharine Carlin at *Catharine.Carlin@oup.com*).

Abstract. Until very recently, research on perceptual organization had been primarily descriptive. The outcome was a taxonomy of phenomena with little attempt to identify underlying mechanisms or develop predictive models. The situation has changed in recent years. New experimental methods have been introduced to measure the organizational processes in vision and other sensory modalities, and new predictive computational theories have been developed. This *Handbook* is an organized survey of the many new approaches to the study of perceptual (mainly visual) organization <u>with an emphasis on modeling</u>. With chapters written by leading authorities, the *Handbook* describes modern experimental and computational methods that not only contribute to deciphering the mechanisms of the classical phenomena of perceptual organization but also open new perspectives in what is sometimes called a neo-Gestalt approach to perception. The intended audience includes researchers in psychology, neural science, computer science, and philosophy as well as graduate and advanced undergraduate students in these fields.

12. Our work on motion perception has shown how the uncertainty principle of measurement affects the global distribution of spatiotemporal sensitivity in the visual system. Dr. Gepshtein collaborates with Dr. Michel Vidal-Naquet of RIKEN Brain Science Institute, Japan, applying a similar approach in a theoretical study of stereoscopic vision. They are presently preparing a first report about this work.

We wish to thank the National Institute of Natural Sciences for their generous support of this collaborative research.

3. References

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