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Processing of complex stimuli and natural scenes in the visual cortex

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A major part of vision research builds on the assumption that processing of visual stimuli can be understood on the basis of knowledge about the processing of simplified, artificial stimuli. Recent experimental advances, however, show that a combination of responses to simplified stimuli does not adequately describe responses to natural visual scenes. The systems performance exceeds the performance predicted from understanding its basic constituents. This highlights the fact that the visual system is specifically adapted to the properties of its everyday input and can only fully be understood when probed with naturalistic stimuli.

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Current Opinion in Neurobiology 2004, **14**:1–6

This review comes from a themed issue on
Sensory systems
Edited by Catherine Dulac and Benedikt Grothe

0959-4388/\$ – see front matter
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DOI 10.1016/j.conb.2004.06.002

Abbreviations

RF receptive field
nCRF non-classical receptive field
V1 primary visual cortex

Introduction

Understanding visual processing ultimately amounts to understanding the processing of everyday visual scenes. In the early years of vision research, the significance of interpreting the processing of visual stimuli in terms of their behavioral relevance was well understood [1,2]. Nevertheless, much vision research in the subsequent years has rested on one assumption: the way the brain processes visual stimuli can be understood in terms of the responses to very simple constituent patterns of visual stimuli. Thus, responses to natural stimuli should be adequately described on the basis of responses to more

artificial laboratory stimuli. Consequently, most experiments conducted in the past decades have relied on using simplified artificial stimuli. Starting with the work of Hubel and Wiesel [3] important insight has been obtained by using these stimuli. Models arising from such studies continue to shape the way we think about hierarchical information processing in the visual system [4].

However, recent experiments challenge this belief. For example, in a categorization task a qualitative difference between typical laboratory stimuli and natural stimuli has been demonstrated [5**]. Classification of typical laboratory stimuli requires attentional resources, whereas classification of the natural stimuli can be done in the near absence of attention. Experiments like this bring our focus back on exploring visual processing using behaviorally relevant stimuli. As a consequence of this increased interest in using more naturalistic stimuli, a number of important steps towards the understanding of the processing of everyday stimuli have been made. In fact, using natural stimuli in vision experiments has become an important branch of vision science, as highlighted by the number of recent reviews [6–9]. Here, we discuss recent experimental and theoretical advances on different levels of visual processing. On the level of single neurons much experimental progress has been made on mapping receptive fields using natural stimuli and on characterizing contextual effects. On the level of populations, the encoding of visual stimuli and effects of stimulus structure have been studied. On the theoretical side, we take on a Bayesian point of view and emphasize studies relating the statistics of natural stimuli to properties of cortical cells and studies relating this to psychophysical phenomena.

Mapping receptive fields using complex stimuli

To analyze the role a neuron takes in the process of extracting information from visual stimuli the concept of a receptive field (RF) is often employed. The RF can be defined as a filter modeling the neuron's transformation of the stimulus and can be used for a mathematical description of the neuron's response. A popular method known as reverse correlation has been developed to measure the RF on the basis of the responses to a predefined set of stimuli [10]. This approach has been remarkably successful at describing neurons in the lateral geniculate nucleus [11,12] and the primary visual cortex (see DeAngelis *et al.* [13] for a review). The stimuli used in these studies, however, were of simple structure and constructed to act optimally in concert with the RF mapping technique.

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One popular stimulus for mapping RFs is called 'pixel white noise': the luminance of each pixel on a screen is chosen randomly and independently of all other pixels in the same or any other stimulus frame.

Receptive field maps with natural stimuli

If the hypothesis that visual processing can be understood based on the responses to very simple stimuli is correct, then similar RF maps should be obtained when the neurons are probed with more natural stimuli. However, with the classical reverse correlation technique it is not possible to use natural stimuli for methodological reasons: the correlations inherent to natural stimuli spoil the obtained RF estimate [14]. In contrast to the pixel white noise, which is random in space and time, the pixel luminance in natural stimuli can be correlated over large spatial ranges and long time scales. These correlations, which form the basis of the structure in natural images, lead to spurious structures in the RF estimates. Recently, a number of techniques to overcome this problem have been devised [15^{*},16,17^{**},18]. Willmore and Smyth [19] offer a detailed description of the different approaches together with a quantitative comparison. Applying such a method to data from monkey primary visual cortex V1, Ringach and co-workers [15^{*}] could measure the RFs of simple and complex cells using natural movie clips. The obtained RFs are qualitatively similar to those obtained with randomly flashed gratings. This general notion has been confirmed using a slightly different method of analysis [17^{**}]. The preferred orientation and spatial frequency of the neurons could be predicted by the RF map obtained from natural stimuli. These results support the hypothesis that it is indeed possible to understand the processing of natural scenes in terms of the responses to simple constituents.

However, some results of the above studies do not support this conclusion. Although qualitative properties of neural responses were the same when probed with natural or artificial stimuli, there were quantitative differences. Smyth *et al.* [17^{**}] first determined the RFs with one set of natural scenes and then used these to predict the neural responses to a novel set of natural stimuli. Interestingly, for many cells the predicted response systematically deviated from the measured response in a nonlinear way. Although there is no detailed explanation for this deviation from the linear model, it seems likely to be due to the influence of parts of the stimulus falling outside the classical RF, so-called 'contextual effects'.

Context effects

The response to a stimulus placed within the classical RF of a neuron can be modulated by placing a second stimulus either within or outside the classical RF. The region where a second stimulus does not generate a response by itself, but modulates the response to the first stimulus placed within the classical RF is known as the

non-classical RF (nCRF). Context effects have been extensively studied and a diverse range of these have been described (see Allman *et al.* and Fitzpatrick [20,21] for a review). A recent study sought to classify these effects [22^{*}]. But instead of finding a unified picture of contextual effects, the authors came up with a different point of view: responses to combinations of orientations might be a more fundamental property than the response to a single orientation alone. One basis for this hypothesis is that even cells that do not seem to be orientation tuned when probed with a single stimulus do show a modulation of their response when exposed to orientation contrasts. Furthermore, the authors demonstrated that spatial position of the two orientations is crucial in determining the response modulation. Taken together, this leads to the conclusion that cells in V1 might be engaged in a more complex task than just extracting information about a single orientation within the RF. Instead, neurons seem to measure the local orientation context, defined by the orientation and placement of different features. Indeed, considering the complex arrangement of oriented contours in natural scenes, such a detection of orientation context might be more meaningful and efficient.

In a complementary study, Dan and co-workers [23^{*}] used a reverse correlation technique with oriented stimuli to probe response properties of complex cells. These so-called random bar (not random dot) stimuli allowed the identification of relevant features and null features. The relevant features activated a neuron and when several of these were shown simultaneously, they interacted additively. By contrast, the null features evoked no response when presented in isolation. However, they had a divisive effect on the response induced by concurrently presented optimal features. This demonstrates nicely how parts of a stimulus, which have no visible effect by themselves, exert an important influence on the overall response properties of these neurons.

These results imply that the response properties of a neuron can only be fully characterized if the entire RF plus surround are stimulated with realistic natural stimuli. This is also supported by experiments that study the influence of stimulus size on the coding efficiency and information transfer in V1 of awake monkeys [24,25] (but see Weliky *et al.* [26^{**}] for a negative result on this). Vinje and Gallant [24,25] compared the responses to a stimulus confined within the classical RF and to stimuli covering increasing amounts of the nCRF. When both the classical RF and the nCRF were stimulated, the neurons conveyed more information about the stimulus, the neurons selectivity increased, and the information was transmitted with increasing efficiency. Thus, these results support the notion that V1 neurons are specifically adapted to the properties of natural scenes and operate efficiently under such natural conditions in a way that

cannot be predicted from studying the RF using simple stimuli only.

Coding on the population level

Higher processing stages are not influenced by single V1 neurons alone but by the activity of a larger population. This leads to the question of how relevant such efficient coding on the single neuron level is and whether single neurons provide a good estimate about a natural stimulus. A recent study [26**] compared the responses of single V1 neurons to a population code built on the responses of many recorded neurons. These investigators measured the tuning properties of the recorded neurons using classical stimuli and used these in a contrast energy model to predict the responses to natural images. Such a contrast energy model [27] describes the firing rate based only on the frequency spectrum of the stimulus and discards the phase structure. As the responses recorded in this study were mostly phase invariant, the contrast energy model is a reasonable approach in this situation. For single neurons, the predicted responses correlated weakly with the measured responses. For a population average based on the responses of overlapping RFs, by contrast, the predicted response correlated well with measured responses. Thus, on the population level, a linear pooling mechanism can be used to extract the local contrast information of the stimulus. The authors furthermore demonstrated that this population code has similar sparseness and efficiency properties to the single neurons. This indicates that on the population level the picture might be less complex than on the level of single neurons. However, as the contrast energy model used to predict the responses is only based on the Fourier amplitudes of the RF and stimulus it does not address the influence of higher order stimulus statistics on the responses.

In view of this result, it seems worthwhile to study the properties of V1 population responses in more detail, especially the influence of the statistical properties of the stimulus. A recent study addressed this issue by measuring population responses in V1 of awake cats [28*]. The responses to natural movies and to pink noise (see below for an explanation of pink noise) stimuli having the same frequency spectrum as the original movies were indistinguishable. These pink noise stimuli were generated from natural movies by randomizing the phases of the different frequencies in the Fourier space; the frequency spectrum in contrast was not manipulated. As a result these stimuli have the same frequency content, but are random otherwise. Thus, V1 population responses do not seem to be sensitive to this higher order structure, which makes the difference between the noise and the natural movie. However, using stimuli with altered second order properties and thus different frequency content, such as drifting gratings, the induced response patterns were markedly different. These results demonstrate a qualitative difference in the

response properties to classical laboratory stimuli and complex stimuli.

Statistical approaches

As progressively more complicated methods are used for analyzing the responses of neurons to natural stimuli, it becomes necessary to come up with good predictions and models of how the visual system processes its everyday input. To achieve this, statistical methods, especially the Bayesian approach, seem to be helpful: our sensors do not provide perfect knowledge about the world and we are thus forced to generate estimates about sensory stimuli in the presence of noise; prior knowledge about the typical sensory environment helps to generate good estimates. There are two approaches in which Bayesian statistics have been helpful at understanding visual processing. First, they can be used to predict neural properties optimal for extracting useful information from natural stimuli. Second, they can be used to predict behavioral data and decisions from the knowledge about natural stimuli.

Such Bayesian processing is not only of interest for neuroscience research and understanding the brain but also for the design of computer algorithms and artificial vision systems (for related reviews see Oram *et al.*, Lee and Mumford, and Srivastava *et al.* [29–31]).

Encoding of information by single neurons

For the first approach, it is necessary to make assumptions about which information is meaningful for the visual system and which information is noise. In view of experimental results showing that cells in V1 produce sparse activity patterns upon stimulation with natural scenes, a common assumption is that meaningful stimuli have a sparse distribution. On the basis of this assumption it has been shown that simple cells in the primary visual cortex can be understood as optimally encoding patches of natural scenes in a linear fashion [32,33]. Using a different assumption, that meaningful information varies slowly over time, it was possible to uncover a close relation between the properties of complex cells in V1 and the properties of natural stimuli [34,35]. In these studies, a model for the neurons' activity was specified *a priori* and only the impact of the parameters of the linear RFs was investigated. However, this approach is not limited to linear models or models with an *a priori* fixed nonlinearity. Actually, the parameters controlling the neuron's nonlinearities also can be optimally adapted to the statistics of natural scenes. Recent studies have made progress in this direction by showing how the exponent controlling the output nonlinearity of complex cells can be optimized simultaneously with the linear RF kernels [36] or by having a hierarchy of nonlinear levels [37].

Recently, such nonlinearities in the responses of single neurons have been investigated experimentally [38]. The

authors used a sequence of random bars, a reasonably complex but well controlled stimulus, to study the RF properties of complex cells in V1. By fitting neural networks to the recorded responses, the authors confirmed the standard model for complex cells used in theoretical studies. Furthermore, estimations of the exponent of the output nonlinearities provided the experimental counterpart to the theoretical results in Kayser *et al.* [36], showing that the theoretical results replicated the neuronal properties well.

The flexibility of this theoretical approach allows it to be used to make quantitative predictions about the properties of neurons in higher cortical areas that are not well characterized yet. However, in contrast to V1, the properties of neurons in higher areas are not fixed after development but can change during learning of novel tasks [39]. Thus, although the properties of V1 neurons are determined for optimal extraction of general features from natural stimuli, the relevant features for higher-level neurons might change during an organism's lifetime. A very nice demonstration of such an effect was provided recently by Rainer *et al.* [40^{*}]. In this study, monkeys were trained to discriminate among a set of natural images, some of which were degraded by noise. The authors were able to demonstrate that the training recruited a significant proportion of neurons to extract the relevant stimuli from the noise patterns. By contrast, the responses of these neurons to undegraded stimuli did not change. Thus, for these neurons the relevant features were the stimuli to be discriminated in the task, and the neurons were optimized during training to extract these images from the noise filled background. On the basis of these assumptions, one should be able to reproduce this experiment in the context of theoretical models as described above.

Behavior explained by the statistical properties of natural scenes

Following the second approach, Bayesian methods can be used to predict the performance of the nervous system as a whole [41]. Consider, for example, the problem of estimating the speed of movement of a striped object that we see through an aperture. We cannot know its exact speed of movement. We might, however, know that objects typically move slowly across our visual field. And indeed, Weiss *et al.* [42^{**}] have demonstrated using psychophysical work that human estimates can be explained by a Bayesian system using the *a priori* knowledge that lower speeds are more likely than higher speeds. A similar link between the occurrence of color in natural scenes and the psychophysical color context effects was established [43]. The same laboratory similarly showed that our perception of depth is related to the occurrences of physical depth in our natural environment [44]. Thus, our sensory processing and perception use *a priori* knowledge about the typical properties of natural stimuli to infer the most likely stimulus configuration.

A recent study provided a demonstration of an adaptation of the visual system to the typical orientation content of natural scenes [45]. Typically, horizontal and vertical structures are more prominent in natural scenes than oblique orientations. Our sensitivity is highest to oblique orientations, and therefore we amplify 'untypical' structures in natural scenes. If probed with gratings, however, the opposite result is found. This highlights not only an adaptation of the visual system to properties of natural scenes but also that this adaptation can only be uncovered when natural stimuli are used in the experiments.

Conclusions

If the brain is optimally adapted to the complex real world scenes that we encounter in our everyday life, then we should be particularly good at processing them. And indeed, complex or natural stimuli are more efficiently classified than simple geometrical shapes [5^{**}]. Furthermore, the processing of complex images can be very fast [46] and can proceed in parallel [47]. Taken together, this evidence gives strong support for the theory that the brain can only be fully understood when it is processing its natural and everyday input. In the future we expect to see more studies demonstrating such qualitative differences between simplified and natural stimuli. In particular, studies in other sensory modalities could confirm that this property holds throughout sensory cortex. Similarly, the technical insights gained, for example, in mapping receptive fields using complex stimuli, will prove helpful not only for other stages in the visual hierarchy but for other sensory systems as well. But to prevent the experimental data from being a simple collection of facts, more theoretical work is needed linking properties of sensory stimuli, behavioral parameters, and properties of the brain. Such theoretical work ultimately could reveal functional principles common to different sensory systems and thus provide a more unified picture of sensory processing.

Acknowledgements

The authors have been supported by the Swiss National Science Foundation (P König), the Neuroscience Center Zurich (C Kayser), and the Wellcome trust (KP Körding).

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