

# A natural approach to studying vision

Gidon Felsen & Yang Dan

**An ultimate goal of systems neuroscience is to understand how sensory stimuli encountered in the natural environment are processed by neural circuits. Achieving this goal requires knowledge of both the characteristics of natural stimuli and the response properties of sensory neurons under natural stimulation. Most of our current notions of sensory processing have come from experiments using simple, parametric stimulus sets. However, a growing number of researchers have begun to question whether this approach alone is sufficient for understanding the real-life sensory tasks performed by the organism. Here, focusing on the early visual pathway, we argue that the use of natural stimuli is vital for advancing our understanding of sensory processing.**

The visual system is a remarkable device, able to process complex spatiotemporal patterns of light signals collected by the eyes and provide information about a rapidly changing world, which is essential for the survival of the organism. The efficiency of the visual circuit is not accidental; it has been shaped by the forces of evolution and refined during development in an experience-dependent manner. The function of the system is thus intimately related to the properties of the visual stimuli commonly found in the natural environment. Much of what we know about visual processing has been obtained from studies using 'artificial' stimuli, including parametric sets of simple stimuli (such as spots of light or sinusoidal gratings) and stimulus ensembles with simple statistics (for example, white noise). However, recent studies have begun to incorporate 'natural' stimuli, such as photographs or video recordings of the natural environment<sup>1</sup>. Here, before assessing how the use of natural stimuli can advance our understanding of visual processing, we will first examine the strengths and weaknesses of the commonly used artificial stimuli.

## Artificial stimuli

Well-designed simple stimuli have been pivotal to elucidating the neural basis of sensory processing. In the visual system, simple stimuli such as spots or bars of light have revealed the receptive field (RF) structure of retinal<sup>2</sup> and thalamic<sup>3</sup> neurons and the orientation selectivity of cortical neurons<sup>4</sup>, which constitute the foundation of modern vision research. A major advantage of these stimuli is that

they are readily parameterized and therefore ideal for determining the dependence of the neuronal response on a particular stimulus parameter (for example, orientation of the bar), often represented as a tuning curve. However, these simple stimuli have a significant drawback: in the natural environment, sensory inputs rarely consist of isolated simple patterns. Because neuronal processing is largely non-linear, the responses to the natural stimuli are often poorly predicted by the sum of the responses to the individual simple components. Thus, studies using simple stimuli alone do not necessarily tell us how a neuron responds to the more complex stimuli encountered in the natural environment.

Another approach is to use a large set of random stimuli, which allows exploration of a larger stimulus space and a more comprehensive characterization of the neuronal response properties. By identifying the set of stimuli that precede neuronal spiking (the 'spike-triggered' stimulus ensemble) and comparing it with the entire stimulus ensemble presented in the experiment, one can identify the features of the stimuli that influence the neuronal response. In particular, white noise, which contains equal power at all frequencies and no spatiotemporal correlation, has been used to measure the spatial and temporal RFs of early visual neurons<sup>5</sup>. Although this statistical property of white noise is highly desirable for systems identification in general<sup>6</sup>, in practice it is often ineffective for driving sensory neurons, particularly in later processing stages, making it difficult to estimate the RF parameters accurately. Sparse random stimuli, which consist of a rapidly presented, random sequence of preselected stimulus patterns, can be more effective than dense white-noise stimuli for measuring certain response properties<sup>7–10</sup>. However, the choice of stimulus set in each experiment requires prior assumption about what stimulus parameters are functionally relevant for the cell being studied, which may result in biases in the interpretation of the experimental results.

Given the limitations of the simple and random stimuli, natural stimuli provide a valuable complement for the study of visual processing. Compared to simple, parametric stimulus sets, the use of natural stimulus ensembles requires fewer a priori assumptions about relevant stimulus parameters. Compared to white noise, natural stimuli are functionally more relevant and, in some cases, more effective for driving the neurons<sup>11,12</sup>. Furthermore, because many sensory neurons show adaptation and contextual modulation, the response properties measured with artificial stimuli may not generalize to natural stimuli; certain properties may be apparent only under natural stimulation<sup>13</sup>. Although analyzing responses to natural stimuli may not be as straightforward as for the artificial stimuli, new methods are being developed to overcome these complications<sup>11,13–17</sup>. Indeed, recent studies using natural stimuli have yielded new insights into the function of the visual system.

Gidon Felsen is at the Cold Spring Harbor Laboratory, 1 Bungtown Road, Cold Spring Harbor, New York 11724, USA. Yang Dan is in the Department of Molecular and Cell Biology and the Helen Wills Neuroscience Institute, University of California Berkeley, Berkeley, California 94720-3200, USA.  
e-mail: ydan@berkeley.edu

Published online 23 November 2005; doi:10.1038/nn1608

### What natural stimuli have taught us

Arguably, to establish the functional significance of a response property characterized with artificial stimuli, this property should be validated under natural stimulation. If a response property does not contribute to explaining the responses to natural stimuli, its functional relevance in visual processing must be limited—even if the property is prominent under artificial stimulation. Conversely, the extent to which a given model explains the responses to natural stimuli provides an essential measure of the completeness of the model. Such validation analyses have been performed at several stages of the early visual pathway. For example, in the lateral geniculate nucleus (LGN), neuronal RFs measured with white noise have been used to predict the responses to natural stimuli. The prediction based on the linear spatiotemporal RF alone captured the basic temporal features of the responses to natural stimuli<sup>18</sup>. In the primary visual cortex, neuronal RFs were originally characterized with spots or bars of light<sup>4</sup>. Simple cell RFs were found to contain oriented ON and OFF subregions; complex cell RFs were modeled as the combination of multiple simple cell RFs with the same orientation preference but different ON-OFF locations. Recently, several studies have examined the structure of cortical RFs by analyzing the neuronal responses to natural images. Using spike-triggered average for simple cells<sup>15</sup> and spike-triggered covariance<sup>11</sup> or other nonlinear methods<sup>14,17</sup> for complex cells, these studies showed that the RFs of V1 neurons during natural stimulation are similar to those measured with the simple or white-noise stimuli. Together, these studies have largely validated the basic spatial structure of early visual RFs measured with artificial stimuli.

In addition to verifying the RF models measured with artificial stimuli, natural stimuli have been used to reveal properties that were not predicted by the results of previous experiments. In a recent study<sup>13</sup>, the RFs of visual cortical neurons in awake behaving monkeys were estimated from the recorded responses to both natural stimuli and dynamic gratings, and the RF structures were found to be affected by both the spatial and temporal statistics of the stimuli. Under natural stimulation, the RF showed a significant inhibitory component that was not observed in the responses to the artificial stimuli; moreover, the RF estimated with natural stimuli predicted the responses to a separate set of natural stimuli more accurately than did the RF estimated with artificial stimuli. Thus, natural stimuli have helped us to reveal a functionally relevant response component that has evaded characterization with artificial stimuli.

Another example of a response property uniquely revealed by natural images comes from a study on cortical feature sensitivity—the ability of each neuron to detect the presence of its preferred features in the visual inputs<sup>12</sup>. By analyzing the cortical responses to ensembles of random stimuli, natural images and synthetic stimuli with either natural power or natural phase spectra, this study showed that the sensitivity of complex cells is higher when the feature is present in natural images than when it is present in random stimuli. Notably, this enhanced feature sensitivity was due to the phase spectra of natural images rather than to their power spectra, and it was not predicted by the standard models of complex cells<sup>4,19,20</sup>, which were derived from studies using artificial stimuli. This finding suggests that complex cells are functionally more specialized than described by the standard models; they respond more vigorously to the oriented edges and contours commonly found in natural images than to the random stimuli that, according to the standard model, should have activated them to the same extent. Of course, once this response property is revealed, one can design parametric, artificial stimulus sets (for example, sums of sinusoids with various phase relationships<sup>21</sup>) to further characterize this property. However, without the use of natural images, it would have been difficult to discover such a property in the

first place. In addition to this example in the visual system, response properties that are specifically tuned to the statistics of natural stimuli have also been demonstrated in the auditory system<sup>22,23</sup>.

Finally, studies on the statistics of natural stimuli have addressed the functional significance of a range of neuronal response properties previously characterized with artificial stimuli. For example, natural visual stimuli contain extensive spatial<sup>24</sup> and temporal<sup>25</sup> correlations (for instance, neighboring pixels tend to have similar luminance values), which gives rise to a high degree of redundancy in the input signals. Quantitative analyses of these correlations show that the center-surround antagonism of the spatial RFs<sup>26,27</sup> and the biphasic impulse response functions<sup>28</sup> of retinal and LGN neurons are well suited for decorrelation of natural stimuli, which significantly reduces the coding redundancy<sup>29</sup>. In the primary visual cortex, reducing redundancy by maximizing the statistical independence of the responses of neighboring neurons (rather than through simple decorrelation) depends on a form of contrast gain control that resembles the well-known divisive normalization model<sup>20</sup>. This gain control can account for a variety of cortical response properties such as cross-orientation suppression and tuning for stimulus size<sup>30</sup>. Related to redundancy reduction, another well-known conjecture of visual processing is sparse coding<sup>31</sup>, in which each stimulus elicits robust responses in only a small number of neurons<sup>31,32</sup>. Notably, when response sparseness (or, similarly, statistical independence) of a population of model neurons was maximized under natural stimulation, the RFs of these model neurons resembled those of cortical simple cells—in terms of both spatiotemporal profile<sup>33–35</sup> and chromatic properties<sup>36</sup>. By demonstrating the functional advantages of particular response properties, these theoretical studies have addressed the question of why the neurons respond the way they do. This line of research thus complements the experimental investigations that focus primarily on how the neurons respond.

### Challenges in the use of natural stimuli

The results described above have demonstrated that a combination of theoretical and experimental studies using natural stimuli can lead to new insights into visual processing. However, there are considerable challenges in the use of natural stimuli, which makes the skepticism of some researchers understandable. To make natural stimuli a more useful tool for vision research, we believe it is necessary to address the following major issues.

Most theoretical studies of natural stimulus statistics have thus far led to explanations of known response properties rather than to predictions of new properties. Predictions usually count more than explanations, an intuitive notion that has also been endorsed by philosophers of science<sup>37</sup>. Although explaining the existing observations may be safer and less likely to be challenged, ‘sticking one’s neck out’ with bold predictions is more likely to make a strong impact. From the experimentalists’ point of view, the most attractive predictions are those that not only provide a rigorous test of a particular computational theory, but also lead to potential findings that are surprising in their own right, with functional or mechanistic implications reaching beyond the original theory. A good example of such a prediction comes from a recent study, in which independent component analysis (a method for maximizing coding efficiency<sup>34</sup>) was applied to the outputs of model V1 complex cells. The result predicted that, to represent step edges in images, each V2 neuron pools the responses of V1 neurons that have similar preferred orientations and RF locations but different spatial frequencies<sup>38</sup>. In another study, a hierarchical probabilistic model was used to learn higher-order statistical regularities in natural images. This algorithm yielded representations of abstract image properties such as object location, scale and texture<sup>39</sup>,

which may reflect the response properties of extrastriate visual cortical neurons. Such predictive modeling studies are highly valued by the experimental community.

In experimental studies using natural stimuli, a major difficulty is the analysis of the stimulus-response relationship, owing to the complex statistical properties of natural stimuli. In general, estimation of RFs involves correlating the stimulus and the response, which is relatively straightforward if the stimulus is Gaussian white noise<sup>6</sup>. Unfortunately, natural stimuli are neither white nor Gaussian, which can cause inaccuracies in the RF estimation. Although some properties of natural stimuli have been well characterized (for example, the predominance of low-frequency signals resulting from spatial and temporal correlations), their higher-order regularities are not well understood. For instance, although it has long been recognized that the phase structure of natural images is far from random and is important perceptually<sup>40</sup>, only a few studies have addressed the phase structures of natural images<sup>41,42</sup>. A better understanding of these regularities in natural stimuli will greatly facilitate unbiased experimental characterization of neuronal response properties using natural stimuli.

At a more basic level, even the concept of 'natural stimuli' has not been defined rigorously. For example, scenes from city streets and forest environments are likely to have different statistical properties, such as the distribution of oriented energy<sup>43</sup>. Each species may be specifically adapted to its own natural environment, and even the same visual circuit may function differently when stimulated by different types of natural scenes. Yet, in most studies, the stimuli are 'natural' only from a human perspective, and the selection of images in the stimulus ensemble is largely arbitrary. In an effort to overcome such a limitation, one study used video cameras attached to the heads of freely roaming cats to record visual stimuli natural to the cat<sup>44</sup>. The resulting stimuli indeed appear quite different from those selected from a standard Hollywood production, with a larger representation of the visual objects closest to the ground and temporal dynamics reflecting the head and body movements of the cat. Similar studies have been performed on several other species<sup>45–47</sup>. To make future experimental studies more fruitful, it would be useful to standardize natural stimuli and to categorize them into subclasses based on functionally relevant statistical properties. There are multiple criteria to consider, such as whether the stimuli are indigenous to the natural environment of the particular animal and whether sampling of the stimuli reflects the body, head and eye movements of the animal during natural behavioral tasks. Although there may not exist a simple and obvious set of classification criteria, the field is likely to benefit from some level of standardization.

## Conclusion

In summary, we believe that physiological experiments using natural stimuli and guided by theories derived from natural stimulus statistics constitute a powerful approach to understanding the visual system. Although in this article we have focused on the early visual pathway, the response properties of higher cortical neurons (that is, those beyond V1) are likely to be even more closely associated with the characteristics of natural stimuli<sup>48</sup>. Predictions of these properties based on natural stimulus statistics combined with experiments using ecologically relevant stimuli may prove to be indispensable for cracking the neural code in higher visual areas. In addition to the response properties of single neurons, the measurement of ensemble neuronal responses to natural stimuli—using multielectrodes<sup>49</sup> or optical methods—may also reveal new principles of visual processing. Thus, despite the challenges, natural stimuli are bound to be critical in advancing our understanding of visual processing.

## ACKNOWLEDGMENTS

We thank F. Han, J. Touryan, B. Willmore and W. Vinje for helpful comments. This work was supported by a grant from the National Eye Institute (R01 EY12561).

## COMPETING INTERESTS STATEMENT

The authors declare that they have no competing financial interests.

Published online at <http://www.nature.com/natureneuroscience/>  
Reprints and permissions information is available online at <http://npg.nature.com/reprintsandpermissions/>

1. Simoncelli, E.P. & Olshausen, B.A. Natural image statistics and neural representation. *Annu. Rev. Neurosci.* **24**, 1193–1216 (2001).
2. Hartline, H.K. The receptive fields of optic nerve fibers. *Am. J. Physiol.* **130**, 690–699 (1940).
3. Hubel, D.H. & Wiesel, T.N. Integrative action in the cat's lateral geniculate body. *J. Physiol. (Lond.)* **155**, 385–398 (1961).
4. Hubel, D.H. & Wiesel, T.N. Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *J. Physiol. (Lond.)* **160**, 106–154 (1962).
5. Reid, R.C., Victor, J.D. & Shapley, R.M. The use of m-sequences in the analysis of visual neurons: linear receptive field properties. *Vis. Neurosci.* **14**, 1015–1027 (1997).
6. Marmarelis, P.Z. & Marmarelis, V.Z. *Analysis of Physiological Systems: The White-Noise Approach* (Plenum, New York, 1978).
7. Ringach, D.L., Hawken, M.J. & Shapley, R. Dynamics of orientation tuning in macaque primary visual cortex. *Nature* **387**, 281–284 (1997).
8. Mazer, J.A., Vinje, W.E., McDermott, J., Schiller, P.H. & Gallant, J.L. Spatial frequency and orientation tuning dynamics in area V1. *Proc. Natl. Acad. Sci. USA* **99**, 1645–1650 (2002).
9. Felsen, G. *et al.* Dynamic modification of cortical orientation tuning mediated by recurrent connections. *Neuron* **36**, 945–954 (2002).
10. Bredfeldt, C.E. & Ringach, D.L. Dynamics of spatial frequency tuning in macaque V1. *J. Neurosci.* **22**, 1976–1984 (2002).
11. Touryan, J., Felsen, G. & Dan, Y. Spatial structure of complex cell receptive fields measured with natural images. *Neuron* **45**, 781–791 (2005).
12. Felsen, G., Touryan, J., Han, F. & Dan, Y. Cortical sensitivity to visual features in natural scenes. *PLoS Biol.* **3**, 1819–1828 (2005).
13. David, S.V., Vinje, W.E. & Gallant, J.L. Natural stimulus statistics alter the receptive field structure of V1 neurons. *J. Neurosci.* **24**, 6991–7006 (2004).
14. Ringach, D.L., Hawken, M.J. & Shapley, R. Receptive field structure of neurons in monkey primary visual cortex revealed by stimulation with natural image sequences. *J. Vis.* **2**, 12–24 (2002).
15. Smyth, D., Willmore, B., Baker, G.E., Thompson, I.D. & Tolhurst, D.J. The receptive-field organization of simple cells in primary visual cortex of ferrets under natural scene stimulation. *J. Neurosci.* **23**, 4746–4759 (2003).
16. Sharpee, T., Rust, N.C. & Bialek, W. Analyzing neural responses to natural signals: maximally informative dimensions. *Neural Comput.* **16**, 223–250 (2004).
17. Prenger, R., Wu, M.C., David, S.V. & Gallant, J.L. Nonlinear V1 responses to natural scenes revealed by neural network analysis. *Neural Netw.* **17**, 663–679 (2004).
18. Dan, Y., Atick, J.J. & Reid, R.C. Efficient coding of natural scenes in the lateral geniculate nucleus: experimental test of a computational theory. *J. Neurosci.* **16**, 3351–3362 (1996).
19. Adelson, E.H. & Bergen, J.R. Spatiotemporal energy models for the perception of motion. *J. Opt. Soc. Am. A* **2**, 284–299 (1985).
20. Heeger, D.J. Normalization of cell responses in cat striate cortex. *Vis. Neurosci.* **9**, 181–197 (1992).
21. Mechler, F., Reich, D.S. & Victor, J.D. Detection and discrimination of relative spatial phase by V1 neurons. *J. Neurosci.* **22**, 6129–6157 (2002).
22. Rieke, F., Bodnar, D.A. & Bialek, W. Naturalistic stimuli increase the rate and efficiency of information transmission by primary auditory afferents. *Proc. Biol. Sci.* **262**, 259–265 (1995).
23. Woolley, S.M., Fremouw, T.E., Hsu, A. & Theunissen, F.E. Tuning for spectro-temporal modulations as a mechanism for auditory discrimination of natural sounds. *Nat. Neurosci.* **8**, 1371–1379 (2005).
24. Attneave, F. Some informational aspects of visual perception. *Psychol. Rev.* **61**, 183–193 (1954).
25. Dong, D.W. & Atick, J.J. Statistics of natural time varying images. *Netw. Comput. Neural Syst.* **6**, 345–358 (1995).
26. Srinivasan, M.V., Laughlin, S.B. & Dubs, A. Predictive coding: a fresh view of inhibition in the retina. *Proc. R. Soc. Lond. B* **216**, 427–459 (1982).
27. Atick, J.J. Could information theory provide an ecological theory of sensory processing? *Netw. Comput. Neural Syst.* **3**, 213–251 (1992).
28. Dong, D.W. & Atick, J.J. Temporal decorrelation: a theory of lagged and nonlagged responses in the lateral geniculate nucleus. *Netw. Comput. Neural Syst.* **6**, 159–178 (1995).
29. Barlow, H.B. Possible principles underlying the transformation of sensory messages. In *Sensory Communication* (ed. Rosenblith, W.A.) 217–234 (MIT Press, Cambridge, Massachusetts, USA, 1961).
30. Schwartz, O. & Simoncelli, E.P. Natural signal statistics and sensory gain control. *Nat. Neurosci.* **4**, 819–825 (2001).
31. Field, D.J. What is the goal of sensory coding? *Neural Comput.* **6**, 559–601 (1994).
32. Willmore, B. & Tolhurst, D.J. Characterizing the sparseness of neural codes. *Network* **12**, 255–270 (2001).

33. Olshausen, B.A. & Field, D.J. Emergence of simple-cell receptive field properties by learning a sparse code for natural images. *Nature* **381**, 607–609 (1996).
34. Bell, A.J. & Sejnowski, T.J. The “independent components” of natural scenes are edge filters. *Vision Res.* **37**, 3327–3338 (1997).
35. van Hateren, J.H. & Ruderman, D.L. Independent component analysis of natural image sequences yields spatio-temporal filters similar to simple cells in primary visual cortex. *Proc. R. Soc. B Biol. Sci.* **265**, 2315–2320 (1998).
36. Caywood, M.S., Willmore, B. & Tolhurst, D.J. Independent components of color natural scenes resemble V1 neurons in their spatial and color tuning. *J. Neurophysiol.* **91**, 2859–2873 (2004).
37. Lipton, P. Testing hypotheses: prediction and prejudice. *Science* **307**, 219–221 (2005).
38. Hyvarinen, A., Gutmann, M. & Hoyer, P.O. Statistical model of natural stimuli predicts edge-like pooling of spatial frequency channels in V2. *BMC Neurosci.* **6**, 12 (2005).
39. Karklin, Y. & Lewicki, M.S. Learning higher-order structures in natural images. *Network* **14**, 483–499 (2003).
40. Oppenheim, A.V. & Lim, J.S. The importance of phase in signals. *Proc. IEEE. Inst. Electr. Electron. Eng.* **69**, 529–541 (1981).
41. Thomson, M.G. Beats, kurtosis and visual coding. *Network* **12**, 271–287 (2001).
42. Wang, Z. & Simoncelli, E.P. Local phase coherence and the perception of blur. in *Advances in Neural Information Processing Systems*, Vol. 16 (eds. Thrun, S., Saul, L. & Scholkopf, B.) (MIT Press, Cambridge, Massachusetts, USA, 2003).
43. Coppola, D.M., Purves, H.R., McCoy, A.N. & Purves, D. The distribution of oriented contours in the real world. *Proc. Natl. Acad. Sci. USA* **95**, 4002–4006 (1998).
44. Kayser, C., Einhauser, W. & Konig, P. Temporal correlations of orientations in natural scenes. *Neurocomputing* **52**, 117–123 (2003).
45. Passaglia, C., Dodge, F., Herzog, E., Jackson, S. & Barlow, R. Deciphering a neural code for vision. *Proc. Natl. Acad. Sci. USA* **94**, 12649–12654 (1997).
46. Lewen, G.D., Bialek, W. & de Ruyter van Steveninck, R.R. Neural coding of naturalistic motion stimuli. *Network* **12**, 317–329 (2001).
47. Lei, Y. *et al.* Telemetric recordings of single neuron activity and visual scenes in monkeys walking in an open field. *J. Neurosci. Methods* **135**, 35–41 (2004).
48. Tanaka, K. Inferotemporal cortex and object vision. *Annu. Rev. Neurosci.* **19**, 109–139 (1996).
49. Fiser, J., Chiu, C. & Weliky, M. Small modulation of ongoing cortical dynamics by sensory input during natural vision. *Nature* **431**, 573–578 (2004).