Stable Receptive Field Structure of Color Neurons in Primary Visual Cortex under Adapting and Non-adapting Conditions

Bevil R. Conway, Department of Neurobiology, Harvard Medical School, Boston MA 02115. bconway@hms.harvard.edu

Abstract

The way in which color signals from the three cone classes (L, M, S) are handled by the rest of the visual system to bring about color perception is incompletely known. In particular, the neural mechanism underlying two fundamental features of color vision, color contrast and color constancy, are unclear. Modeling efforts have shown that these features could be accounted for by neurons capable of making chromatic comparisons across visual space. The existence of such neurons in the primate is contested. I revisited the issue, recording the activity of single neurons in primary visual cortex of alert macaques trained to fixate a dot on a computer monitor, on which I flashed small spots of light that modulated a single cone class at a time. Cone-isolating stimuli can either increase or decrease one of the three cone types, thus there are a total of 6 stimuli; the stimuli were presented on a neutral gray adapting background. I correlated the location of the spots with the neural activity to produce receptive field maps. A fraction of neurons had both spatially and chromatically structured receptive fields. These were compared with receptive fields determined using stimuli presented on different-colored high-contrast (non-adapting) backgrounds. Receptive-fields with high-contrast stimuli had the same shape, but were slightly larger (10%) and had slightly shorter (5ms) latencies. These "double-opponent" neurons respond best to color contrast and could be the building blocks for color constancy.

Introduction

Some parvocellular neurons, located in the lateral geniculate nucleus early in visual processing, show opposite responses to opponent colors [1], a response attributed to opponent input from the cones [2] (Figure 1). Receptive fields of parvocellular neurons tend to be circularly symmetric, giving opposite responses in the center and the periphery: the center may be excited by red and the surround inhibited by green [3]. For these parvocellular neurons, the *weakest* stimulus would a stimulus with very high color contrast, e.g. a red spot on a green background. The particular balance in intensity of red to green that produces the weakest response can be called the "equiluminance null point". There are several types of parvocellular neurons and each type has a slightly different equiluminance null point [4, 5].

Parvocellular neurons have been grouped into three categories, L vs. M, L+M vs. S and +(L, M, S) vs. –(L, M, S), which were once thought to underlie the cardinal color axes red-green, blue-yellow and black-white. But the categorization appears to be somewhat arbitrary [6] [7] and does not reflect cardinal hues [8]. The basis for cardinal colors remains a mystery. In fact, the role of parvocellular neurons in color vision also remains mysterious because they respond worst to precisely the stimulus one would expect a color cell to be most sensitive to, a high color-contrast stimulus [9]. It has been argued that the main contribution of parvocellular neurons to vision is therefore not color, but sensitivity to high-resolution form. In this regard, the cone inputs that make up the excitation of the center of the "L-ON" and "M-ON" neurons (indicated by triangles and Xs on a white background in Figure 1) are irrelevant; what is important is that both give excitatory discharges to increases in light, i.e. both are sensitive to tiny light spots on a dark background.

Neurons of the lateral geniculate nucleus send their signals to neurons in primary visual cortex. Each neuron in primary visual cortex receives several inputs [10], which results in receptive fields that have more elaborate structure, for example orientation-selective simple cells, which respond best to a bar of light at a given orientation [11](Figure 1). The spatial structure of the receptive fields of simple cells is organized into distinct sub-regions, so that the neurons respond best to one particular spatial frequency of a sine-wave grating. Simple cells are thought to arise by the orderly connection of lateral geniculate inputs [3, 10], and are thought to be critical for the detection of luminance edges. A given "ON"-center simple cell, responding best to a white bar on a black background, gets input from several "ON"-center lateral geniculate neurons, possibly of both L-ON and M-ON varieties. Simple cells are then thought to send their outputs to complex cells [11]. Complex cells also respond well to edges, but their receptive fields show no spatial structure. Presumably this is because they receive inputs from many simple cells, of both "ON" and "OFF" varieties.

Many neurons in primary visual cortex, perhaps the majority, do not have an equiluminance null [4, 12, 13]. Presumably this is because each cortical neuron receives input from many geniculate cells, each with a different null point; these different inputs compensate for each other: a particular balance of red:green, that nulls one input, excites an adjacent input. The lack of an equiluminance null point has been taken as a necessary feature of a color neuron.

But lacking an equiluminance null is not sufficient to indicate that a neuron is contributing to color vision. Many psychophysical observations show that there are other important features of color, including color opponency and a lack of response to white [14], [15]. The riddle of contemporary color neurophysiology is that most neurons in primary visual cortex, even those that lack an equiluminance null, do not exhibit these features [16]. This could be because these neurons pool together inputs from a variety of parvocellular neurons, constrained by the sign of the center response, ON or OFF, but not by the cone type (in Figure 1, the ON-simple-cell inputs are all white, but two are triangles and one is an X).

The solution to the riddle may be that color vision is sub-served by only a tiny fraction of neurons in visual cortex, which could be missed in large surveys. Indeed one might predict that color requires only a small number of neurons, given the crumby resolution of color vision relative to form vision [17]. With this in mind, I have been investigating the properties of only those neurons in primary visual cortex that exhibit explicit cone-

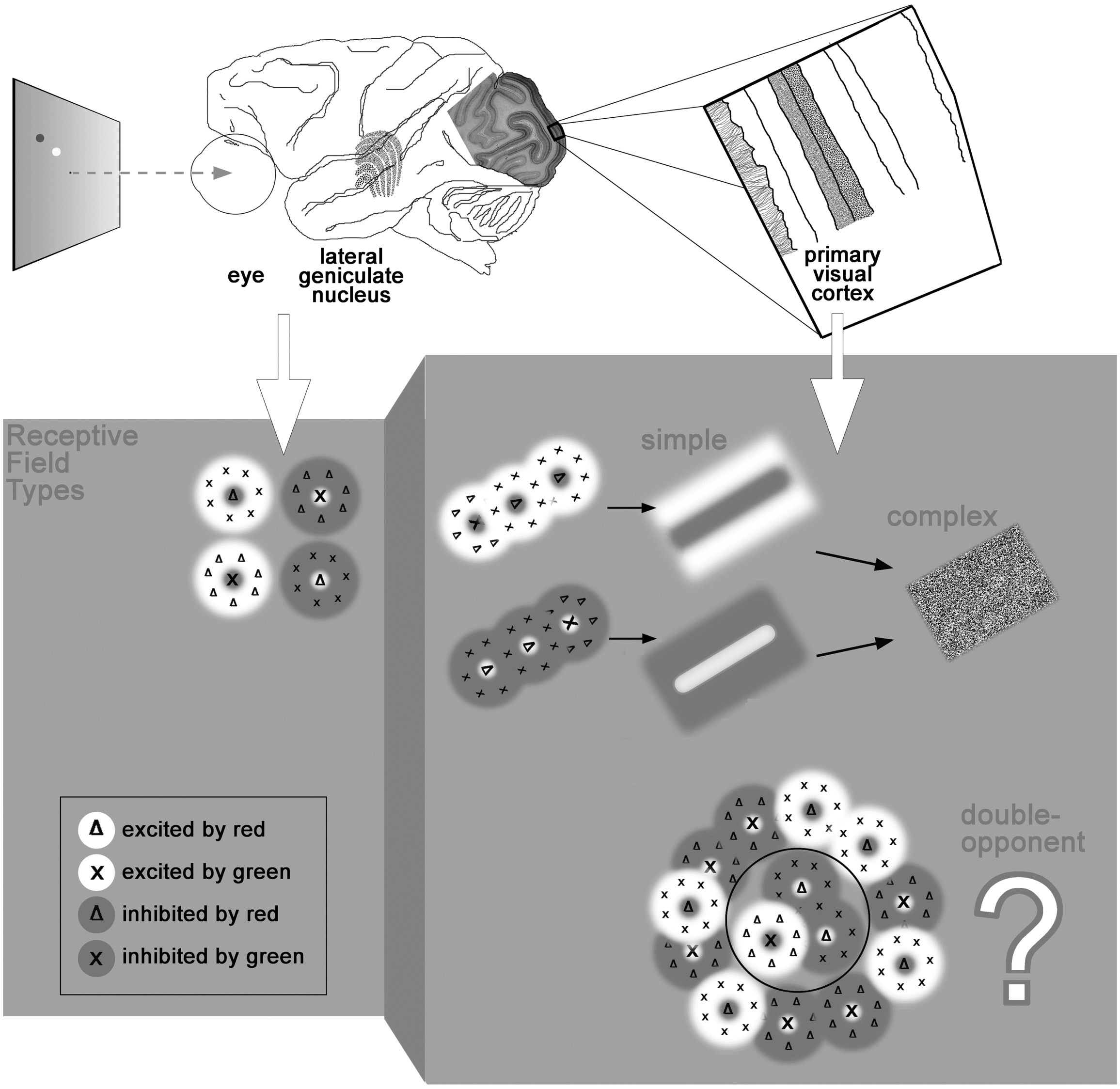

Figure 1. *Receptive fields of neurons in the parvocellular layers of the lateral geniculate nucleus (LGN) and primary visual cortex (V1). LGN neurons are the building blocks for receptive fields in V1. One question centers on the existence of neurons in V1 with double-opponent receptive fields. Such receptive fields are both chromatically opponent and spatially opponent (hence “double”). Note that simple cells have spatial luminance opponency but not chromatic opponency; i.e. a given simple cell could combine different types of LGN cells, so long as the centers of the LGN cells are all either excitatory or inhibitory.*

opponency: that show excitation to one cone type and suppression to another (e.g. excitation to red and suppression to green). Such cells are rare, perhaps only 10% [18].

Double Opponent Receptive Fields

One feature of color vision invented by the brain is color contrast – that red looks redder against green. It has been argued that this, and the related problem of color constancy, could be partly resolved by a neural mechanism that makes simultaneous chromatic comparisons across space [19]. “Double-opponent” neurons capable of such comparisons have been found in the goldfish retina [20], but their existence in the primate visual system has been contested (hence the “?” in Figure 1, see [18] for a review). The cone inputs to primate primary visual cortical neurons have been mapped and support the conclusion that many cone-opponent neurons are double-opponent [18], having spatially offset receptive field sub-regions, with opposite chromatic opponency. Such neurons are simple-like because their receptive fields show spatial structure.

But it has since been argued [21] that the stimuli used in these experiments were inadequate because they employed non-adapting conditions; the spatial structure observed is rationalized as just an artifact of the non-adapting stimulus. Other recent studies have failed to find double-opponent neurons [22], implying that simple-like double-opponent neurons do not exist. Thus it is argued that color calculations depend on complex neurons that respond at equiluminance and are spatial-frequency tuned; this implicates most primary visual cortex neurons in both color and form calculations. Although it may be tempting to call these complex-equiluminance neurons “double-opponent” [22], because they show both spatial-frequency and chromatic tuning, the wiring required to bring them about would seem to be fundamentally different from that required to bring about simple-like, proper double-opponent neurons. So it is probably worth distinguishing them, regardless of their role in color.

Because simple-like double-opponent neurons are critical

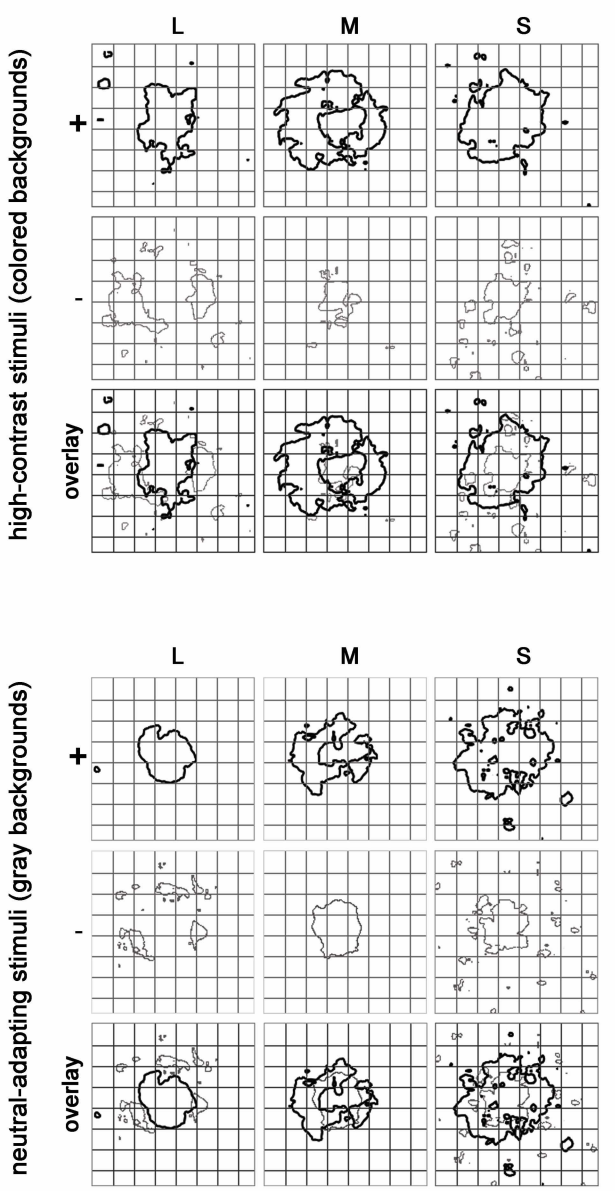

*Figure 2. Spatial receptive field of a single cone-opponent neuron in primary visual cortex measured with high-contrast cone-isolating stimuli (top) and neutral-adapting stimuli (bottom). The receptive field shape is preserved under both conditions although the receptive field is slightly larger under high-contrast conditions. Grid shown to enable a comparison; small divisions are 0.75 degrees. Stimuli were 0.6 degrees square and were not constrained by the grid. Cone modulation index (CMI) = ((maximum cone activity - minimum cone activity)/(maximum cone activity + minimum cone activity)) * 100. CMI (M, L, S, top) = 50, 50, 96; CMI (M, L, S, bottom) = 34, 34, 94. Methods are described in [18]; Stockman and Sharpe (2000) cone fundamentals were used [33].*

to many models of color vision (e.g. [23-29]; complex-equiluminant cells do not seem to do the trick), I revisited the issue of their existence. I recorded the activity of single neurons in primary visual cortex of alert macaques, trained to fixate a spot on a computer monitor while small spots of cone-isolating light were flashed at different locations on the screen (all procedures were similar to those in [18]). Cone-isolating stimuli modulate a single cone class at a time by using the method of silent substitution [30]. Cone activity is dependent on two

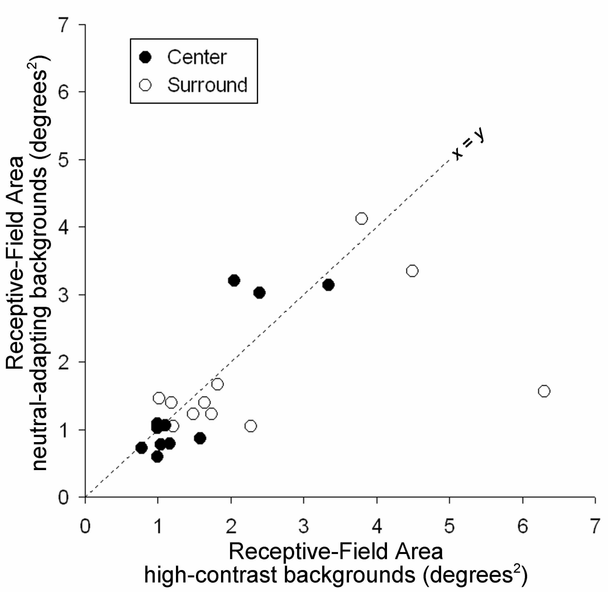

Figure 3. Receptive field extent of cone-opponent neurons in primary visual cortex measured with high-contrast stimuli versus neutral-adapting stimuli. The center of all neurons were within the central 5 degrees.

variables, intensity and wavelength. Because each cone class has a broad absorption spectrum, almost any wavelength (or combination) can be used to drive a given cone class to the same degree, simply by appropriately adjusting the intensity. Thus two stimuli can be determined that produce identical cone activity in two of the three cone types, but modulate the third. Six cone-isolating stimuli can be made, each either increasing (+) or decreasing (-) the activity of one of the three cone types.

Cone-isolating stimuli can be developed using a neutral gray adapting background, or they can be developed by using different colored backgrounds for each stimulus [18]. Using colored backgrounds yields higher cone contrast, but as Shapley and Hawken (2002) point out, has the disadvantage of being non-adapting. We know so little about the properties of cortical cone-opponent neurons, so this disadvantage is hard to evaluate. Here I used stimuli on gray backgrounds. I determined the spatial structure of the receptive fields of 37 cone-opponent neurons. Many showed double-opponent structure, which will be described in detail in a future report. Here I compare the responses to neutral-adapting stimuli with those to high-contrast stimuli for a subset of these neurons (Figure 2; Figure 3). The spatial maps for all six stimuli have been plotted separately, with a contour line indicating the response >2*standard deviation above the background. Figure 2 (top) shows the receptive fields generated under high-contrast conditions; Figure 2 (bottom) shows the receptive fields under neutral-adapting conditions, for a single neuron. The receptive fields under both conditions were similar: critically the surround response in the neutral-adapting condition (the M+, L- maps) was clearly significant, revealing a spatially and chromatically opponent simple-like doughnut receptive-field structure. Figure 3 quantifies the results of all cells examined in this way. The spatial extent of the receptive fields under high-contrast conditions were about 10% larger (y=0.9x, r^2=0.74, single outlier removed). The latencies to peak were also slightly faster, by 5 ms (+/-3ms).

Conclusion

Neurons function under a range of physical conditions that is greater than the range of possible neural responses – for example a neuron can have a firing rate of up to ~500Hz, but ambient natural light levels can vary over several orders of magnitude. The brain deals with this problem through receptoral and neural adaptation [31]. How do putative color neurons in the visual system, specifically in primary visual cortex, respond under different adaptation states? The conclusion that neurons in primary visual cortex have double-opponent spatial structure [18] was based on responses of neurons to stimuli with different backgrounds; the adaptation state of the neurons was not constant. The conclusion that the receptive fields were double-opponent therefore begged the question of whether neurons have stable receptive fields under different adaptation states. If not, then can one conclude that the neurons are actually double opponent? Here I show that the receptive fields are largely stable under different adaptation conditions, indicating that they are suitable building blocks for color constancy and color contrast calculations. In contrast, the chromatic tuning of the majority of complex-equiluminance cells varies with contrast [31], making them less suitable building blocks for color vision. Thus several lines of evidence are converging on the conclusion that color vision is sub-served by a relatively small fraction of neurons in primary visual cortex, which have rather specialized receptive field features. Perhaps by investigating the structure, chromatic tuning and cone inputs of these neurons in greater detail we will make headway in understanding the neural basis for cardinal hues and establish a neural basis for color space. This will hopefully guide studies of color vision in downstream extrastriate color areas like V4 and PITd [32].

References

[1] R. L. De Valois, I. Abramov, and G.H. Jacobs, Analysis of response patterns of LGN cells. Journal of the Optical Society of America, 56(7), 966-77 (1996).

[2] R.C. Reid, nd R.M. Shapley, Space and time maps of cone photoreceptor signals in macaque lateral geniculate nucleus. J. Neurosci., 22(14), 6158-75 (2002).

[3] T.N. Wiesel and D.H. Hubel, Spatial and chromatic interactions in the lateral geniculate body of the rhesus monkey. J. Neurophysiol., 29, 1115-1156 (1966).

[4] D.H. Hubel and M.S. Livingstone, Color and contrast sensitivity in the lateral geniculate body and primary visual cortex of the macaque monkey. J. Neurosci., 10(7), 2223-37 (1990).

[5] N.K. Logothetis et al., Perceptual deficits and the activity of the color-opponent and broad-band pathways at isoluminance. Science, 247(4939), 214-7 (1990).

[6] A.K. Romney, R.G. D'Andrade, and T. Indow, The distribution of response spectra in the lateral geniculate nucleus compared with the reflectance spectra of Munsell color chips. Proc. Natl. Acad. Sci. U S A, 102(27), 9720-5 (2005).

[7] B.R. Conway and M.S. Livingstone, A different point of hue. Proc. Natl. Acad. Sci. U S A, 102(31), 10761-2 (2005).

[8] S.M. Wuerger, P. Atkinson, and S. Cropper, The cone inputs to the unique-hue mechanisms. Vision Res, 45(25-26), 3210-23 (2005).

[9] D. Hubel and M. Livingstone, Color puzzles. Cold Spring Harbor Symposia on Quantitative Biology, 55, 643-9 (1990).

[10] R.C. Reid and J.M. Alonso, Specificity of monosynaptic connections from thalamus to visual cortex. Nature, 378(6554), 281-4 (1995).

[11] D.H. Hubel and T.N. Wiesel, Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. J. Physiol., 160, 106-154 (1962).

[12] P. Gouras and J. Kruger, Responses of cells in foveal visual cortex of the monkey to pure color contrast. J. Neurophysiol., 42(3), 850-60 (1979).

[13] E.N. Johnson, M.J. Hawken, and R. Shapley, The spatial transformation of color in the primary visual cortex of the macaque monkey. Nature Neuroscience, 4(4), 409-16 (2001).

[14] L.M. Hurvich, Color vision (Sinauer Associates Inc., Sunderland, MA, 1981).

[15] S.J. Schein and R. Desimone, Spectral properties of V4 neurons in the macaque. J. Neurosci., 10(10), 369-89 (1990).

[16] P. Lennie, J. Krauskopf, and G. Sclar, Chromatic mechanisms in striate cortex of macaque. J. Neurosci., 10(2), 649-69 (1990).

[17] M.S. Livingstone and D.H. Hubel, Psychophysical evidence for separate channels for the perception of form, color, movement, and depth. J. Neurosci., 7(11), 3416-68 (1987).

[18] B.R. Conway, Spatial structure of cone inputs to color cells in alert macaque primary visual cortex (V-1). J. Neurosci., 21(8), 2768-83 (2001).

[19] E.H. Land, Recent advances in retinex theory and some implications for cortical computations: color vision and the natural image. Proc. Natl. Acad. Sci. U S A,. 80(16), 5163-9 (1983).

[20] N. Daw, Goldfish retina: organization for simultaneous color contrast. Science, 158, 942-944 (1968).

[21] R. Shapley and M. Hawken, Neural mechanisms for color perception in the primary visual cortex. Curr. Opin. Neurobiol., 12(4), 426-32 (2002).

[22] S.G. Solomon, J.W. Peirce, and P. Lennie, The impact of suppressive surrounds on chromatic properties of cortical neurons. J. Neurosci., 24(1), 148-60 (2004).

[23] E.H. Land, The retinex theory of color vision. Scientific American, 237(6), 108-28 (1977).

[24] D.I. Flitcroft, A neural and computational model for the chromatic control of accommodation. Vis. Neurosci., 5(6), 547-55 (1990)..

[25] P.A. Dufort and C.J. Lumsden, Color categorization and color constancy in a neural network model of V4. Biological Cybernetics, 65(4), 293-303 (1991).

[26] E. Doi et al., Spatiochromatic receptive field properties derived from information-theoretic analyses of cone mosaic responses to natural scenes. Neural Comput., 15(2), 397-417 (2003).

[27] D.H. Foster, S.M. Nascimento, and K. Amano, Information limits on neural identification of colored surfaces in natural scenes. Vis. Neurosci., 21(3), 331-6 (2004).

[28] A. Hurlbert and K. Wolf, Color contrast: a contributory mechanism to color constancy. Prog. Brain Res., 144,147-60 (2004).

[29] H. Spitzer and Y. Barkan, Computational adaptation model and its predictions for color induction of first and second orders. Vision Res., 200. 45(27), 3323-42 (2004).

[30] O. Estevez and H. Spekreijse, The "silent substitution" method in visual research. Vision Res., 22(6), 681-91 (1982).

[31] S.G. Solomon and P. Lennie, Chromatic gain controls in visual cortical neurons. J. Neurosci., 25(19), 4779-92 (2005).

[32] B.R. Conway and D.Y.Tsao, Color Architecture in Alert Macaque Cortex Revealed by fMRI. Cerebral Cortex, December 28 (first published on-line) (2005).

[33] A. Stockman and L.T. Sharpe, Tritanopic color matches and the middle- and lon-wavelength-sensitive cone spectral sensitivities. Vision Res., 40, 1739-1750 (2000).

Author Biography

Bevil Conway received his PhD in neurobiology (Harvard University ,2001), and is a Junior Fellow in the Harvard Society of Fellows and an Alexander von Humboldt Research Fellow (Bremen University). www.bevilconway.com.