Accuracy of subspace mapping of spatiotemporal frequency domain visual receptive fields

Shinji Nishimoto¹, Miki Arai¹, Izumi Ohzawa¹,²

1 Graduate School of Engineering Science,  
2 Graduate School of Frontier Biosciences,  
Osaka University,  
1-3 Machikaneyama, Toyonaka, Osaka 560-8531, Japan

Correspondence should be addressed to:

Izumi Ohzawa  
Graduate School of Frontier Biosciences and School of Engineering Science  
Osaka University  
1-3 Machikaneyama, Toyonaka, Osaka 560-8531 Japan

Telephone: +81-6-6850-6520  
Fax: +81-6-6850-6557  
Email: ohzawa@fbs.osaka-u.ac.jp
Abstract

Orientation and spatial frequency selectivities are fundamental properties of cells in the early visual cortex. Although they are customarily tested with drifting sinusoidal gratings, a recently developed subspace reverse correlation method (Ringach et al., 1997a) may be a better replacement for obtaining a selectivity map in a joint orientation and spatial frequency domain at higher resolution efficiently. These two methods are examined for their accuracy and data compatibility for cells in areas 17 and 18 of anesthetized and paralyzed cats. Peaks and bandwidths of tuning curves from these two methods are highly correlated. However, spatial frequency bandwidths obtained by reverse correlation tend to be slightly narrower for the subspace reverse correlation than those from the drifting grating tests. Consistency between the two methods is improved, if the entire duration of data containing signal are taken into account for the subspace reverse correlation, rather than using the map only at the optimal correlation delay. Examination of convergence of the subspace mapping process shows that reliable 2-d profiles can be obtained within 5 – 10 min. for the majority of cells. Temporal dynamics of tuning properties are also examined more directly with the subspace mapping than with the drifting gratings. For many cells, the optimal spatial frequency shifts substantially, measured as a fraction of tuning bandwidth, over the time course of response. In comparison, the optimal orientation remains highly stable throughout the duration of response. Overall, these results suggest that the subspace reverse correlation is a better substitute for the conventional method.
Introduction

Orientation and spatial frequency selectivities are two of the most prominent characteristics of neurons in the primary visual cortex (Hubel and Wiesel 1962; Campbell et al. 1969; Maffei and Fiorentini 1973; Movshon et al. 1978a; De Valois et al. 1982). As these characteristics of the stimuli determine predominantly the overall strength of a cell’s responses, measurements of these selectivities are essential when one performs electrophysiological experiments in these areas, regardless of the primary experiments that follow. Traditionally, measurements of these tuning characteristics have been performed primarily by using drifting sinusoidal gratings. Substantial body of existing physiological data, both published and unpublished, are in these forms. However, recent advances in receptive field mapping techniques have made alternative techniques possible for measuring these fundamental tuning properties, in the form of subspace reverse correlation (Ringach et al. 1997a) which is fast becoming a new standard for basic characterization of neurons (Ringach et al. 1997b, 2003; Mazer et al. 2002; Felsen et al. 2002; Bredfeldt and Ringach 2002; Sugihara et al. 2004). How accurate is the new method, considering the speed at which measurements are completed? How do data obtained by the new methods compare with those obtained by the traditional techniques? And if they differ, how and where do differences arise? Answers to these basic questions are important in establishing the basis upon which results from future studies are compared reliably with previous findings.

With the traditional method using drifting sinusoidal gratings, the parameter for one of the dimensions (e.g., orientation) is varied while those of other dimensions (e.g., spatial frequency) are fixed. The orientation and spatial frequency tunings thus obtained (typical forms of these tunings are in Figs. 1A and 1B) are, however, essentially cross-sections of a two-dimensional tuning surface of a joint orientation and spatial
frequency domain (Fig. 1C). Tuning characteristics for off-the-peak cross-sections have not
been measured traditionally (with a few exceptions, e.g., Jones and Palmer 1987b), and
one-dimensional sequential measurements described above might miss the overall peak in
the surface. Although the entire 2-D tuning surface can theoretically be obtained by drifting
gratings, it simply takes too long to execute in practice. Furthermore, simultaneous
measurement from many neurons is increasingly becoming common recently (Maldonado
Weliky et al. 2003), but the traditional tuning measurement is not conducive for these
situations. This is because the orientation is fixed for measuring the spatial frequency
tuning, hence only a subset of neurons, whose preferred orientations are close to the
stimulus orientation, could be excited in a given measurement.

The subspace reverse correlation, exploiting flash grating stimuli of various
orientation of spatial frequency, can measure the two-dimensional tuning surface in
experimentally reasonable testing time (Ringach et al. 1997a, 2003; Mazer et al. 2002;
Sugihara et al. 2004). What remains to be shown is how accurately results of the
conventional tests using drifting gratings and those of the subspace mapping technique
agree. Do peaks or bandwidths of the parameters match between the two methods? Is there
any tendency for the match to be better depending on the cell type or on other properties of
neurons, such as direction selectivity? One of the primary purposes of this study is to assess
compatibilities between the two methods with the intent of replacing conventional
measurements by drifting gratings with subspace reverse correlation mapping. In what
follows, we will show the following: (1) Estimates of preferred orientation and spatial
frequency are generally matched well for the two methods. (2) Bandwidths of the spatial
frequency tunings tend to be narrower for the subspace mapping than that for the drifting
gratings. (3) Classification of simple and complex cells, traditionally based on the degree of
modulation in responses to drifting gratings, is also possible using subspace reverse correlation by a ratio of responses to stimuli of antagonistic phases. (4) For the majority of the cells, reliable 2-d profiles can be obtained only by 5-10 min. of stimulations. Therefore, results from the current study provide the basis upon which physiological data from new studies may be compared directly with those based on the traditional measurements.

**Methods**

All recordings were made from adult cats weighing between 1.5 kg and 4.4 kg. All animal care and experimental guidelines conformed to those established by the National Institute of Health and were approved by the Osaka University Animal Care and Use Committee.

*Surgical procedure and physiological recordings*

After initial preanesthetic doses of hydroxyzine (atarax 2.5mg) and atropine (0.05mg), each cat is anesthetized with isoflurane (2.5-3.5% in O₂). ECG (electrocardiogram) electrodes and a rectal temperature probe are inserted, and a femoral vein is catheterized. Then cefotiam hydrochloride (Panspolin, 8.3µg) and dexamethasone sodium phosphate (Decadron, 0.4mg) were administered. Subsequently, tracheostomy is performed and a tracheal tube is inserted. Then the animal’s head is secured in a stereotaxic device with the use of ear and mouth bars, and clamps on the orbital rim. Tips of the ear bars were coated with local anesthetic gel (Lidocaine). After the securing the animal, a craniotomy is performed directly above the central representation of the visual field in the visual area 17 or 18 (Horsley-Clarke P4 L2.5 for recordings of A17, A3 L3 for A18). The dura is dissected away to allow insertion of microelectrodes. We use tungsten microelectrodes (A-M Systems, 5MΩ) for recording spike activity extracellularly. Typically, two electrodes are used to increase the chance of encountering cells, and they are mounted in parallel in a
single protective guide tube and driven by a common microelectrode drive (Narishige). After lowering the electrodes to the cortical surface, agar is used to protect the cortex, and melted wax is applied over the agar to create a sealed chamber for stabilization. Anesthesia is then switched to sodium thiopental (Ravonal, given continuously 1.0 - 1.5 µg/kg/hr). After stabilization of anesthesia, paralysis is induced with a loading dose of gallamine triethiodide (10-20 mg), and the animal is placed under artificial respiration at the rate of 20-30 strokes per min. The respiration rate and stroke volume are adjusted to maintain end-tidal CO2 in between 3.5 - 4.3%. Artificial respiration is carried out with a gas mixture of 70% N2O and 30% O2. The infusion fluid thereafter contains Ravonal, gallamine triethiodide (10 mg/kg/hr), and Glucose (80µg/kg/hr) in Ringer’s solution. Body temperature is maintained near 38.3 degrees C with the use of a servo-controlled heating pad. Pupils are dilated with atropine (1%) and nictitating membranes are retracted with phenylephrine hydrochloride (Neosynesin, 5%). Contact lenses with 4 mm artificial pupils are positioned on each cornea.

To record the activity of single units, electrical signals from the microelectrodes are amplified (x10000) and bandpass-filtered (300-5000Hz). Then spike sorting was achieved using a custom-built spike sorter (Ohzawa, et al. 1996), where each spike was sorted by their waveforms and time-stamped with 40 µs resolution.

Visual stimulation and initial procedures

All the experiment control functions and generations of visual stimuli were performed using custom-written software on two Windows PCs. Visual stimuli were generated by a dedicated PC and displayed on a cathode-ray-tube (CRT) display (SONY GDM-FW900, a resolution of 1600 x 1024 pixels, refreshed at 76 Hz). The animal saw the display through a custom-built haploscope, which allows dichoptic presentations of visual stimuli to left and
right eyes separately. Distance (total length of light paths) between the screen and the eyes were set to 57 cm, subtending the visual field of 23 (horizontal) x 30 (vertical) degrees for each eye.

When we encountered isolated action potentials from one or more cells, we performed the following preliminary tests to obtain an accurate center position and a size of the cell’s receptive field. First, we obtain a rough position of the cell’s receptive field by presenting a small circular patch of a drifting sinusoidal grating and controlling the X-Y position of the patch manually by a pointing device (mouse). Then a standard reverse correlation procedure (Jones & Palmer 1978a, DeAngelis, et al. 1993a), and/or a modified reverse correlation procedure (instead of the conventional black/white bars, a small Gabor patch is presented to enhance the cell’s responses) were performed to obtain the accurate position of the receptive field. Position of the visual stimuli throughout this paper is set to the center of the visual field mapped in these tests.

The primary purpose of this study is to assess compatibilities between drifting sinusoidal gratings and subspace reverse correlation technique. Therefore, orientation and spatial frequency selectivities were measured by both subspace reverse correlation and drifting gratings for each isolated cell as described below.

Subspace reverse correlation test

Visual stimulation and analysis in the subspace reverse correlation procedures were equivalent to those used by Ringach, et al. (1997a). Sinusoidal gratings of various orientation, spatial frequency and phase and one blank stimulus were presented in a randomized order, typically lasting for 39 ms (three video frames). Range of orientation was from 0 to 180 degrees in 10-degree steps. Range of spatial frequency was adjusted for each cell to cover the entire frequency range that evoked responses, sampled regularly in
logarithmic scale (typical ranges are $0.02 \text{ – } 0.5$ cycle/degree for cells in area 18, and $0.1 \text{ – } 1.2$ cycle/degree for cells in area 17). Eight to 13 spatial frequencies are used typically. For each combination of orientation and spatial frequency, four phases of gratings, 0, 90, 180 and 270 degrees, were used. Stimulus sets, each of which was a randomized sequence of 577 (8 frequencies x 18 orientations x 4 phases + blank) to 937 (13 frequencies x 18 orientations x 4 phases + blank) gratings, were presented 20-30 times. Evoked responses and the stimulus sequence are then cross-correlated to obtain a 2-dimensional orientation and spatial frequency selectivity map. Spike counts for the blank stimuli are subtracted from the map. We have calculated the maps for correlation delays from 0 ms to 300 ms in 15 ms step, and we hereafter analyze and present a map obtained at the optimal correlation delay that contains the largest signal as in this example, unless otherwise noted.

To make an objective criterion for data selection, we estimated the noise level in the data by computing standard deviations (SD) of selectivity maps with non-causal correlation delays, i.e., maps obtained from stimuli after spikes occurred. Specifically, the SDs of maps for non-causal delays are calculated from $-300 \text{ to } -90$ ms in 15 ms steps, and we rejected the data when the SD at the optimal delay did not exceed the mean + 5 SD of the non-causal maps. For a subset of neurons, to examine temporal dynamics of spatial frequency tunings accurately, we have performed additional experiments with subspace mappings in a specialized configuration as below. For these experiments, the duration of stimulus presentations was shortened to 26 ms from the standard 39 ms to increase temporal resolution, and the orientation of stimuli was restricted to optimal one, i.e., we have measured selectivity of spatial frequency subspace only (Ringach, et al. 1997a; Bredfeldt and Ringach 2002; Nishimoto and Ohzawa 2004). In a typical set of stimulus sequences of this type, a stimulus of a given frequency and phase was presented for 53 times. One experiment for a cell typically contains 15 iterations of a set, lasting about 18
min in total.

**Drifting grating test**

For conventional tests using drifting sinusoidal gratings, orientation and spatial frequency tuning curves were obtained separately. Only one parameter, either orientation or spatial frequency, was varied in a given run while the other parameter was fixed. The gratings were presented in a randomized order and each presentation lasted for four seconds with one second of inter-stimulus-interval. Stimuli for each condition were presented five times, and responses were averaged over the trial period. The ranges of parameters were adjusted such that they were sufficiently wide to cover the entire range of stimuli that could elicit any response. Size and positions of the gratings were identical to the one used in the subspace mapping test.

**Results**

Recordings were made from a total of 371 cells for which the subspace reverse correlation mapping tests were completed (184 cells from area 17, and 187 cells from area 18, in 27 cats). The recorded area is judged based on the coordinates of the electrode penetrations, and cells that may have been recorded from the 17/18 border are not included in the sample above. Of these 371 cells, additional orientation tuning measurements using drifting grating stimuli could be completed with sufficient reliability for 241 neurons. Complete basic set of three experiments including the spatial frequency tuning run could be completed for 226 cells. Of these, 72 cells were classified as simple and 154 as complex, according to the standard criteria (Skottun et al. 1991; Priebe et al. 2004).
Comparison of peak parameters

To compare orientation and spatial frequency tuning characteristics measured with traditional drifting gratings and those by subspace reverse correlation, we first determine the locations of tuning peaks obtained with the two methods. Fig. 2 shows two typical examples of the analysis. Fig. 2A shows a typical two-dimensional selectivity map for an area 18 complex cell obtained with the subspace mapping procedure. The data obtained with 13 spatial frequencies and 18 orientations (10-deg steps) are shown as a contour plot. The position of the center of inner-most contour in Fig. 2A indicates that the optimal grating parameters was about 165 degree for the orientation and 0.2 cycle/degree for the spatial frequency. The vertical and horizontal dashed lines in the Fig. 2A show the values of fixed parameters (spatial frequency and orientation, respectively) used in the tests by drifting gratings. The vertical dashed line is offset slightly to the right of the peak of the 2-d map, indicating that our initial estimate of optimal spatial frequency used for the orientation tuning run (the very first measurement for this cell) was a little too high. These cross sections through the two dimensional map may be compared directly with tuning curves obtained by the drifting grating tests (Fig. 2B for orientation selectivity and 2C for spatial frequency selectivity).

In Figs. 2B and 2C, the symbols and error bars (standard error) depict data obtained by the drifting grating tests, and the solid curves indicate fits to the data by Gaussian functions. The dashed curves indicate curves cut out from the 2-d subspace map (at the dashed lines in Fig. 2A). For both orientation and spatial frequency tuning curves, results from measurements using traditional drifting gratings and subspace reverse correlation are closely similar. The solid and dashed arrows show the peak positions (i.e., the optimal parameters) of the solid and dashed curves, respectively.

Figs. 2D - 2F show another example of the analysis for a complex cell in area 18. In this
case, the tuning curves are similar for orientation, but systematic deviations are found for the spatial frequency tuning in that the responses are greater for drifting sinusoidal grating stimuli than for reverse correlation stimuli at low spatial frequencies. Mainly because of this, the spatial frequency bandwidth also is narrower for the subspace reverse correlation than for drifting gratings.

We have analyzed the distributions of optimal parameters obtained by the two methods for our sample of cells, and Fig. 3 summarizes the results. Fig. 3A compares the optimal orientations estimated by the drifting grating tests (horizontal axis) with those from the subspace mappings (vertical axis). The shapes of the symbol distinguish the recorded area (+ for area 17 and open circle for area 18). The solid diagonal line indicates the perfect match between the two methods, and the dashed line shows the regression line. As is graphically seen, the results from the two methods are highly correlated ($r=0.99$, $N=242$). The histogram in Fig. 3B shows the distribution of differences in optimal orientations between the estimates from the two methods. Most of the differences are within 30 degrees, which is equal to the sampling interval for the drifting grating tests. Similarly, Figs. 3C and 3D show comparisons of the two methods for estimates of optimal spatial frequencies. Again, the results from the two methods are highly correlated ($r=0.97$, $N=226$).

We have also analyzed the distribution of parameters separately for areas 17 and 18 (data not shown). For the optimal spatial frequency, there are systematic differences between the two areas for both drifting grating measurements ($0.46\pm0.31$ cyc/deg ($n=106$) for area 17, $0.16\pm0.08$ cyc/deg ($n=120$) for area 18) and those of subspace mappings ($0.45\pm0.30$ cyc/deg ($n=184$) for area 17, $0.17\pm0.07$ cyc/deg ($n=187$) for area 18). The differences in the optimal frequency are significant for both measurements (two-sample Wilcoxon test, $p<<0.001$) and the trend that these two areas cover different ranges of spatial frequencies are consistent with previous reports (Movshon, et al. 1978b; Issa, et al. 2000). However, the
magnitudes of differences between the two methods did not significantly differ between areas 17 and 18, for both orientation and spatial frequency measurements (two sample Wilcoxon test, p>0.1). Likewise, except for the overall range of spatial frequency tunings, cells in areas 17 and 18 exhibits similar characteristics at least for those properties we have examined in this study. For this reason, hereafter, we show combined results from the two areas, except for scatter plots where individual cells are marked differently depending on the area. Results of statistical analyses for area dependency will be provided whenever appropriate in each section.

Comparison of tuning widths

Next, we have examined the consistency of the sharpness, or the bandwidth, of tunings obtained with the two methods. To compare the bandwidths quantitatively, half-width at half-height (HWHH) were estimated for each tuning curve. Fig. 4A and B summarize the orientation bandwidths for our sample of cells. Again, the results from two methods are highly correlated (r=0.88) and there was no trend that the results from a method tend to exceed that from the other (one sample Wilcoxon test, p>0.1. Fig. 4B).

A different trend is observed for spatial frequency. Fig. 4C and 4D show the comparisons of spatial frequency bandwidth for the two methods. The spatial frequency bandwidth is defined here as the ratio of high-cutoff frequency to the optimal spatial frequency. Note that, in Fig. 4C, there are more symbols below the diagonal dashed line, meaning that, in contrast to the orientation tuning, the spatial frequency bandwidth for the subspace mappings tended to be narrower than those for the drifting gratings on average (one sample Wilcoxon test p<0.01). There was no significant cortical area dependency (17 or 18) in the magnitude of differences between two methods (two sample Wilcoxon test, p>0.1).
Comparisons of modulation ratio

How do the subspace mappings differ from drifting gratings in determining other characteristics of neurons, such as the simple and complex cell types? Modulation of responses to drifting sinusoidal gratings at the temporal frequency of drift is an intuitively striking property of simple cells. Partly for convenience and simplicity, this measure has been used for simple/complex classification in studies that use grating stimuli. To quantify the degree of modulation, modulation ratio (F1/F0 ratio) of cell’s responses to drifting sinusoidal gratings is widely used as a convenient criterion to classify the cells as simple or complex type (Skottun, et al. 1991; Priebe et al. 2004). Although this criterion is challenged recently (Mechler and Ringach 2002), it is nevertheless true that the ratio is highly correlated with the classification of simple and complex types by other criteria. To examine whether the modulation ratio can be predicted from the data obtained by the mappings, we have defined a “modulation index” (MI) for a given condition (i.e., for a given combination of orientation, spatial frequency and correlation delay) using the subspace mapping data as follows:

\[ MI = 2 \times \frac{|R_0 - R_{180}| + |R_{90} - R_{270}|}{R_0 + R_{90} + R_{180} + R_{270}} \]

where \( R_0 \) indicates spike counts for phase \( \theta \) (degrees) for a given combination of orientation and spatial frequency. MI increases when spatially antagonistic stimuli (i.e., \( R_0 \) vs. \( R_{180} \) or \( R_{90} \) vs. \( R_{270} \)) yield antagonistic responses, which is more likely for simple cells. It decreases when stimuli of all the phases elicit similar level of responses, as is common for complex cells. To perform quantitative comparison of the MI and the F1/F0 ratio, we have calculated a MI for the same spatial frequency and orientation as those used to extract
the F1/F0 ratio in the drifting grating tests. If exactly the same condition was not sampled in the subspace mapping, the nearest sample point was used. Fig. 5A shows histograms and a joint distribution of these metrics for the F1/F0 ratio and MI. Correlation coefficient between the two indices was 0.85 (p<<0.001). Fig. 5B shows how drifting gratings classify cells to simple or complex compared with the classification by the subspace mapping. Of 91% (205/226) of cells, the classification of simple/complex type was matched for the subspace mappings and drifting gratings. There was no significant cortical area dependency (17 or 18) for the correlation coefficients (p>0.1).

Efficiency and accuracy of subspace mapping with reverse correlation

How efficient is the subspace reverse correlation method? This is an important question that essentially determines how long it takes for measuring a receptive field reliably in the frequency domain. Fig. 6A shows an example of a progressive refinement of a selectivity map as the subspace mapping progresses over time for a complex cell recorded from area 18. The top-left panel in Fig. 6A is a spatial frequency-orientation map obtained from a single iteration of a randomized stimulus set. The second map is computed using data from the first two iterations, and so on. Thus, a map at the N-th position is obtained by using data from only the first N iterations. A number above each panel shows correlation coefficient between the map for the panel and the final map obtained by using data from all iterations (the bottom-most panel). Each iteration, as noted in the methods, consists of a complete set of all spatial frequencies, orientations, and phases, which are 13, 18, and 4, respectively for most measurements. Therefore, an iteration is typically 37-second long. For this cell, just one iteration of stimulations yields a visible structure in the map, although it is still noisy. After about 10 iterations of the randomized stimulus sequences (about 370 seconds), a smooth structure was obtained with a quality that is casually indistinguishable
from the final map (which required about 1100 seconds). Therefore, for this cell, there was only a marginal improvement in the tuning map after about 8-10 min of testing.

To examine convergence of the selectivity maps during measurement to the final one obtained by the all iterations, we have calculated expected values of the correlation coefficients between the selectivity map obtained by a given number of iterations and the map obtained by full iterations. The expected value of the correlation coefficient for a given iteration count, N, is calculated using a form of a re-sampling method as follows. For each iteration count N, maps are re-sampled N times from the entire map samples (typically 20 or 30 iterations were performed), allowing repetitive use of maps. As preliminary treatments for noise reductions, both the re-sampled and final maps were smoothed by a 3x3-pixel two-dimensional Gaussian filter with the standard deviation equal to the pixel separation. Then, we have calculated correlation coefficients between the re-sampled maps and the final map. We have performed this procedure 100 times for each iteration count N, and defined the mean of the coefficients as the expected value for a given N.

Fig. 6B shows the growth of the expected values for the cell illustrated in Fig. 6A as data from more iterations are included in the analysis. Correlation coefficient monotonically increases and come to a plateau after about 10 min. Therefore, for this cell, the time necessary for reliable measurement of the complete 2-D tuning surface was approximately 10 minutes.

How efficient are subspace reverse correlation measurements for other neurons in our sample? Fig. 7A shows a summary of the convergence analysis for our sample of cells (N= 371) in a format similar to that of Fig. 6B. Each curve represents results for a cell. Although individual curves are not visible due to the density of the curves, the correlation coefficient of 0.9 can be reached within about 10 minutes for the vast majority of neurons. For further clarifying the distributions, Figs. 7B shows distributions of measurement times
necessary to achieve a given value of correlation coefficients. Distributions of measurement times are shown for correlation coefficients of 0.8, 0.9 and 0.95, respectively. For example, Fig. 7B (top) shows that correlation coefficient of 0.8 could be attained within 5 minutes for nearly all cells. However, to reach the level of correlation coefficient=0.95, some neurons had to be stimulated for more than 10 minutes, although more than a half of the neurons still exceeded this level within 5 minutes. Considering that a complete 2-d joint tuning profile in the orientation-spatial frequency domain consisting of 234 (18 orientations x 13 frequencies) frequency components is obtained in 10-15 minutes for nearly all neurons, subspace reverse correlation method is remarkably time efficient. For comparison, based on 4-second trials repeated 5 times per condition, it would have taken 4680 seconds (18 x 13 x 4 x 5) or 78 minutes to measure the same 2-d tuning profile using traditional drifting grating stimuli.

One must use caution in interpreting the increase in correlation coefficients noted above since the re-sampling procedure itself increases correlation with the final map as more maps are used. Because the degree of overlap between re-sampled maps and the final map will increase with N (iteration count), the correlation will also increase with N, even if the maps are purely random without any structure. To estimate the degree to which the increase in correlation is caused by the procedure itself, we conducted a simulation by applying the method to synthetic random noise maps. The result of the simulation is shown as a dashed curve in Fig. 7A (The shaded area indicates ±1 SD of the mean.). As expected, correlation coefficient increases with N up to about 0.7. However, the ranges of correlation values observed for the data from cells were far higher from the value obtained from the random noise simulation. Therefore, although a portion of the increase of correlation coefficients was due to the re-sampling procedure itself, the correlation coefficients may be used as a reliable measure of convergence to the final map.
**Possible sources of discrepancies**

Overall, subspace reverse correlation in the frequency domain and conventional tuning measurements using drifting sinusoidal gratings produce comparable results. In particular, the estimates of optimal orientation and spatial frequency are in close agreement between the two methods. However, there are some differences that still remain. A part of these differences must be due to inherent variability in neural responses, but it is of interest to examine if there are systematic differences that may hinder straightforward comparisons of new and old results. One factor that may contribute to discrepancies is the difference in the extent of temporal integration of responses. For this study so far, we have estimated the orientation and spatial frequency tuning surface only at the optimal time delay in the subspace reverse correlation. Therefore, responses at other time delays are not incorporated into the tuning surface obtained by subspace mapping. However, with drifting grating stimuli, responses are integrated over multiple temporal cycles of stimuli to obtain the response strength. Such a difference does not matter if a neuron's spatial frequency tuning is invariant over the course of the response, as illustrated in Fig. 9A. For this neuron, responses are observed for correlation delays of 25 - 110 ms, during which the optimal spatial frequency remains nearly constant. However, for another neuron depicted in Fig. 9D, the optimal spatial frequency increases from approximately 0.2 to 0.4 cycles/deg (an octave) over the correlation delays of 40 - 90 ms. Similar slants of response maps in the spatial frequency-time domain have been reported by others, both in the cat (Frazor, et al. 2004) and the monkey (Bredfeldt and Ringach 2002; Mazer et al. 2002; Frazor et al. 2004). Likewise, there are several reports concerning the temporal changes of orientation tunings (Ringach et al. 1997b, 2003; Mazer et al. 2002; for review, Shapley et al. 2003), although the results are somewhat controversial.
To examine temporal dynamics of orientation and spatial frequency tuning characteristics, we have summarized temporal change of optimal orientation and spatial frequency in Figs. 8A and B, respectively, for our sample of cells. Each curve indicates changes in the optimal value over the time course of responses for a cell. The horizontal dashed lines indicate the mean bandwidth (±HWHH) for each domain, calculated from our samples (Fig. 4). Figs. 8C and D show distributions of these shifts taken at 40ms after the response onsets indicated as the vertical dashed lines in Figs. 8A and B. The value of 40 ms was selected to cover the initial rising portion of the response which tended to have higher rate of spatial frequency change than later portions of the responses as seen in Fig. 8B. In addition, it could not be made too long for maintaining reasonable cell counts for Figs. 8C and D. While the majority of temporal shifts for the optimal orientation were restricted to a range as small as 5 deg., the shifts of preferred spatial frequency were substantial and biased for low-to-high sequences. The mean preferred orientation shifts for areas 17 and 18 were -1.1±4.6 deg/40ms and -0.16±4.8 deg/40ms, respectively. Neither of these shifts is significantly different from zero (one-sample Wilcoxon test, p>0.05). For the preferred spatial frequency, the mean shifts for areas 17 and 18 were 0.23±0.28 octave/40ms and 0.20±0.28 octave/40ms, respectively. Both of these were significantly different from zero (one-sample Wilcoxon test, p<<0.01). There were no significant differences between the areas 17 and 18 for orientation or spatial frequency shifts (Kolmogorov-Smirnov test, p>0.05).

The standard deviation of the orientation shift was only about 4.7 deg or 17% of the mean orientation bandwidth of 27.5 deg (HWHH; see Fig. 4A), indicating that for most neurons, the preferred orientation remains very stable over the time-course of responses. In comparison, the preferred spatial frequency shifts (in the low-to-high direction) by as much as 0.23 octaves and 0.20 octaves on average for areas 17 and 18, respectively during
the initial 40 ms of the response (see Fig. 8D). This amounts to nearly 40% of the mean spatial frequency bandwidth of 0.56 octaves (see Fig. 4C). If we consider the standard deviation as in the orientation above, the fraction is even larger at 50%. The difference between the orientation shifts and those for the spatial frequency is also apparent in Figs 8A and B, in that all of the curves for the orientation shifts remain well within the two horizontal dashed lines (Fig. 8A), whereas many curves for the spatial frequency shifts cross and go beyond the top horizontal dashed line (Fig. 8B). These characteristics of temporal shifts of tunings might explain the discrepancy observed for spatial frequency measurements as considered further below, but not for orientation tunings.

To examine more precisely whether the temporal integration of tunings can affect discrepancies between the two methods, we have performed additional sets of experiments for spatial frequency tunings. The additional tests were conducted with shorter durations (26ms) for each grating in a randomized sequence and subspace restricted to spatial frequency (with the orientation fixed to the optimal). All the data in Fig. 9 were from these additional experiments (n=39).

To select the portion of the response time course that contains signals, we have calculated root-mean-square (RMS) response amplitude (i.e., standard deviations of spike counts) of the response for each correlation delay between 0 and 300 ms in 5 ms steps. Spike count for the blank stimulus is subtracted from the map at each correlation delay before computing the RMS amplitude. The correlation delay with the maximum RMS response amplitude ($A_{\text{MAX}}$) defines the optimal correlation delay. The baseline noise level is calculated as the RMS response amplitude for the non-causal portion of the response ($A_{\text{NOISE}}$), which may be considered to contain only noise components (See Methods). Using $A_{\text{MAX}}$ and $A_{\text{NOISE}}$, we define a criterion response as $A_{\text{CRITERION}} = 0.3(A_{\text{MAX}} - A_{\text{NOISE}}) + A_{\text{NOISE}}$, which must be exceeded to be counted as signal. The factor, 0.3, is picked
somewhat arbitrarily by subjectively comparing the selected response portions and the response maps (similar to Figs. 9A and 9D) for all neurons. Other criterion values did not alter the results. These portions of the response containing signal are indicated as red bands above the top margin of Figs. 9A and 9D. A black marker in the gray bands indicates the optimal correlation delay. The tuning curve from the multiple correlation delays are then obtained by summing up these tuning curves over the selected time period shown by the gray bands.

As expected, for the cell that showed a constant spatial frequency tuning for all correlation delays (Fig. 9A), no difference is found regardless of whether the optimal correlation delay is used (Fig. 9B) or data from multiple correlation delays are integrated (Fig. 9C). In both Figs. 9B and 9C, the solid curve depicts the fit to data obtained from drifting grating experiments, whereas dashed curve indicates the spatial frequency tuning obtained by reverse correlation. However, for the cell that exhibited a marked spatial frequency shift over the time course of the response (Fig. 9D), the discrepancy in the tuning curves present in Fig. 9E (only the optimal time slide is used) disappears completely if signals from all significant correlation delays are integrated (Fig. 9F).

Figs. 9G and 9H show a summary of the comparisons between estimations from an optimal correlation delay and that from integrated multiple correlation delays. In Fig. 9G, each symbol, circle or x, with a tick represents a difference of spatial frequency width estimated from drifting gratings and subspace map. For each neuron, the center of the symbol indicates the difference calculated from multiple delays and the endpoint of the tick shows the difference calculated from the map at the peak correlation delay. The style of the symbols represents whether these differences are significant (circle) or not (x) (bootstrap re-sampling, p<0.05)(Efron and Tibshirani 1993). For the spatial frequency bandwidth, 12 out of the 39 cells show significant differences depending on whether data at multiple
correlation delays are used or not. For the optimal spatial frequency, 18 out of the 39 cells exhibited differences. The horizontal solid line shows identity line, i.e., perfect match of parameter estimations from drifting gratings and subspace mappings. Therefore, if a tick extends from a symbol outward from the identity line, it indicates improvement of the match by multi-correlation delay integration. On the other hand, if a tick points inward from a symbol toward the identity line, it indicates worsening of the match. An inspection of the plots shows that integrating multiple correlation delays improves, on average, bandwidth estimation of spatial frequency tunings (one sample Wilcoxon test, p<<0.001). However, even after the integration across multiple correlation delays, the trend that bandwidths from subspace mappings are narrower than that from drifting gratings still remains (one sample Wilcoxon test, p<<0.001), as seen by the fact that most of the symbols are above the identity line. For the optimal spatial frequency, analyses from multiple correlation delays also improve estimations on average (one sample Wilcoxon test, p<0.05).

We have also examined possible dependence of discrepancies between subspace mapping and drifting grating tests for other characteristics of neurons, specifically, correlations with modulation ratio (F1/F0), direction selectivity (DSI), signal-to-noise ratio (S/N), and peak firing rate (Fig. 10). As noted earlier, the modulation ratio is highly correlated with simple and complex type classification. As with tuning shift of spatial frequency over time, direction selectivity is also closely related to spatiotemporal integration of responses, and highly direction selective neurons may be expected to exhibit larger discrepancies. Examination of S/N and peak responses is intended for estimating the degree to which variability and responsiveness influence our measurements of orientation and spatial frequency selectivities. The S/N for each cell is defined as the ratio of RMS (root mean square) amplitude for all points in the 2-D subspace correlation map at the optimal correlation delay and mean of RMS amplitude for non-causal correlation delays.
Contrary to our expectation, significant correlations are found only for 3 cases. A small but significant negative correlation is found between the difference of orientation bandwidth and the modulation ratio, indicating that determinations of bandwidth of orientations tend to be more consistent for simple cells than for complex cells. Significant correlations are also found for the difference of peak orientation and the difference of spatial frequency width, as indicated by the dependences on the S/N. The higher the S/N, the more consistent the optimal orientation and frequency bandwidth estimates are for the two methods. These latter two correlations seem to be reasonably expected as a consequence of inherent variabilities in neural responses. Possible implications of these results will be considered below.

**Discussions**

We have shown that spatial frequency and orientation tuning characteristics measured by a relatively new subspace mapping methods generally agree with those obtained by traditional drifting grating measurements. This study therefore establishes a bridge between new and traditional data, assuring validity of comparisons with the accumulated traditional data with new ones obtained now and in the future. In some cases, however, there are differences between the estimates by the two methods. We will consider possible factors that may cause these discrepancies and examine any potential problems.

**Possible sources of discrepancies**

One of the most obvious discrepancies found between the two methods is that the tuning widths tended to be narrower for the subspace reverse correlation than for the
drifting grating tests. Superficially, this seems to be inconsistent with the results of comparison between the orientation tunings obtained by the Fourier transform of simple cell receptive fields from m-sequence stimuli (equivalent to reverse correlation) and by traditional drifting grating tests (Gardner et al. 1999). In their study, the tuning widths from the reverse correlation were broader nearly by a factor of two than those by drifting gratings. Similar biases were found in the spatial frequency tuning as well (DeAngelis et al. 1993b). There are a few factors that are different between these previous experiments and the present study. One is that the simple cell RF mapping by reverse correlation, used in the previous studies, obtains an estimate of a linear receptive field that is independent of output nonlinearity (Gardner et al. 1999; Anzai et al. 1999), whereas the subspace reverse correlation in the frequency domain is not a linearized measurement, as the method simply sums responses to all four phase conditions for a given combination of frequency and orientation. A power-law output nonlinearity (with an exponent of about 2) that follows a linear receptive field has been shown to sharpen the orientation tuning (Anzai et al. 1999; Geisler and Albrect, 1995). For the case of subspace reverse correlation, such a nonlinearity is always in the measurements. Such power-law output nonlinearities also affect measurements by drifting grating stimuli. Therefore, additional factors may be needed to account for generally sharper tuning for subspace reverse correlation mapping. One such possibility is that drifting grating of optimal parameters is a stronger stimulus for the cell, which is able to drive the neuron above the threshold for firing to a greater degree than drifting gratings. Briefly flashed (40 ms) grating stimuli of the same optimal parameters may excite the neuron relatively weakly, making the response more susceptible for the effects of the nonlinear threshold. Consequently, the sharpening of tuning curves may be more pronounced for the subspace reverse correlation than for drifting gratings.

For determining possible causes for discrepancies between the two methods, we
have examined dependence of differences in the estimated parameters on other characteristics of neurons, as shown in Fig. 10. Out of 20 cases examined, only 3 cases showed statistically significant correlation. One is the difference in the orientation tuning bandwidth, which was found to be dependent on F1/F0 ratio, the degree of temporal modulation in response to drifting sinusoidal gratings. The greater the degree of modulation, the more consistent the results from subspace mapping and drifting gratings were. It is puzzling how such a dependence can arise, and we currently do not have a reasonable explanation for this correlation.

Two other cases of dependence of discrepancies between the methods are found for the signal-to-noise ratio for neurons. The greater the S/N, the better the match was for the estimates of preferred orientations and spatial frequency bandwidths by the two methods. This perhaps simply indicates a straightforward relationship where parameter estimation is better for neurons that respond more strongly and consistently. Therefore, from the analyses of Fig. 10, we did not find any other systematic dependence of the degree of match even for such properties as the direction selectivity.

**Convergence tests**

The results of the convergence tests (Figs. 6 and 7) provide an objective criterion for considering how long we should record cell activities to obtain reliable 2-d profiles. Our results show that, for the majority of cells, 5-10 minutes of stimulations are enough to acquire reliable profiles and the longer stimulations do not substantially improve the profiles. The efficiency of the subspace mappings is examined by a simulation study in Ringach’s original paper (Ringach et al. 1997a) and our results provide the first experimental examinations to show the efficacy in terms of actual testing time. The equivalent tests can be applied to another classes of reverse correlation and can essentially
be performed on-line. The results from these tests might be useful information for determining when to terminate recordings from a given set of neurons, and thus to further reduce testing time.

Although we have adopted the correlation coefficient as the convergence metric in this study, this type of convergence tests may be performed using other metrics such as the optimal orientation in principle. However, we did not adopt such a method because the convergence speed depends critically on tuning bandwidths. Neurons with narrower tuning bandwidths tend to converge faster, while those with broader bandwidths tend not to converge. Therefore, it would be difficult to distinguish whether the convergence is due to the true growth of S/N or merely reflects dependence on the bandwidths.

*Temporal dynamics of tuning characteristics*

We have examined the dynamics of optimal orientation and optimal spatial frequency over the time course of responses, and have shown that the preferred spatial frequency shifts upward for substantial number of neurons in both areas 17 and 18. This was not the case for orientation tunings. How do our results compare with those reported by others? Bredfeldt and Ringach (2002) and Mazer et al. (2002) report relevant results regarding spatial frequency shifts over the time course of the responses. The results from these studies (for the monkey) and ours (for the cat) all agree that substantial number of cells in V1 exhibit low-to-high shift of optimal spatial frequency. Unfortunately, the data from these two previous studies are not mutually comparable due to different ways in which they quantified the degree of frequency shifts. Mazer et al. (2002) reports the rate of spatial frequency shift in cycles/deg/ms without noting the initial spatial frequency. This makes the conversion to octave-based metric used by Bredfeldt and Ringach (2002) and by us impossible.
There is also a minor difference between our frequency shift metric and Bredfeldt and Ringach's. They report the total frequency shift in octaves for the entire duration of the response, whereas we calculate essentially the rate of frequency shift evaluated over the initial 40 ms of the responses. We have chosen this metric because the rate of change of spatial frequency is the key parameter for relating neural responses to, for example, the rate of expansion of visual patterns (although such questions are beyond the scope of this study). However, to compare our results to Bredfeldt and Ringach's, we have recalculated the frequency shift metric to match theirs. Based on our results shown in Fig. 8B, total frequency shifts for the entire duration of responses was 0.22±0.38 (1SD) octaves, 0.24±0.37 octaves, for areas 17 and 18, respectively. This is about 35% of 0.62±0.69 (1SD) octaves reported for monkey V1 (Bredfeldt and Ringach, 2002). Therefore, although all studies including ours agree that there is a clear and significant optimal spatial frequency shift from low to high over the time course of the responses, the amount of shift for the cat area 17 neurons were about 1/3 of that for the monkey. It is not known whether there are any contributing factors for this difference other than the species difference.

Frazor and his colleagues (Frazor et al. 2004) also examined the temporal shifts of spatial frequency tunings by presenting static sinusoidal gratings with longer duration (200ms) and inter-stimulus-intervals. Their results show that the mean ratio of spatial frequency shifts was approximately 0.05 octaves/ms, or 2.0 octaves/40ms in a metric compatible to ours. This is an extremely high value compared with our results (0.23 octaves/40ms for area 17 and 0.20 octaves/40ms for area 18) and even those from Bredfeldt and Ringach (2002), which are about three times larger than ours as noted above. As Frazor and colleagues have pointed out in their paper, the difference in the stimulation protocol and the linearity assumption used in the reverse correlation procedure might be the primary factors in explaining the discrepancy. Due to rapid successive presentations of stimuli in the
reverse correlation procedure, responses to multiple stimuli inevitably overlap in time thereby allowing nonlinear interactions, whereas stimuli used by Frazor et al. were delivered with sufficiently long intervals with little possibility of nonlinear interactions. (See Discussion of Frazor et al. 2004). Such nonlinear interactions in the spatial frequency domain will be a topic for further studies.

For orientation dynamics, Ringach and his colleagues (Ringach et al. 2003) provided the distributions of the preferred orientation shifts over the response time courses for monkey V1 (Fig. 8 of Ringach et al. 2003). A compatible analysis of our data shown in Fig. 8A yields the mean ± 1 SD of the shifts as 0.41±4.7 deg and -0.61±5.3 deg for areas 17 and 18, respectively. These standard deviation values appear somewhat smaller than that for monkey V1, based on inspections of their summary histogram (the exact value was not given for the monkey).

Other tuning properties

In this study, we have limited our analyses to the consistency of spatial tuning parameters between the subspace reverse correlation method and traditional drifting grating measurements. Ideally, the comparison should not stop there, and should also be extended to temporal aspects of dynamical neural responses. As Ringach and his colleagues showed in their original paper (Ringach et al. 1997a), a spatiotemporal receptive field may be predicted from a spatiotemporal subspace map under a linearity assumption for simple cells. From these data, we should be able to predict temporal frequency tunings and even forms of PSTHs to the drifting grating stimuli by convolving the receptive field and the stimulus sequences. Unfortunately, we did not obtain temporal frequency tuning curves using drifting grating stimuli necessary for such comparisons. In addition, predictions of relevant spatiotemporal receptive fields are not possible for complex cells, and are difficult for many
simple cells that possess substantial nonlinearities. This is because the spatiotemporal
tuning properties of complex cells are largely determined by linear subunits, and requires
second-order analyses (Movshon et al. 1978c; Szulborski and Palmer, 1990). Such
comparisons of actual data and predictions might provide further insights into
non-linearities embedded in cells’ response generation mechanisms, and will be a topic of
further studies.

Taken together, our results suggest that the new subspace reverse correlation
mapping is able to provide results that are generally as consistent as the traditional method
based on drifting grating stimuli. We have shown that the results from the new method are
directly comparable to the substantial amount of existing data obtained by the traditional
method. In conclusion, therefore, given the high efficiency in terms of recording time and
generality of stimuli that are applicable for all neurons that are recorded from
multi-electrode arrays, the subspace reverse correlation method is highly desirable as a
superior replacement for traditional drifting grating stimuli for initial characterization of
joint orientation and frequency tuning in studies of early visual cortex.

Acknowledgement

We thank our laboratory members, Hiroki Tanaka, Takahisa Sanada, Rui Kimura, Kota
Sasaki, Masayuki Fukui and Masashi Iida, who participated in recording sessions. This
work was supported by grants 15029230 and the Project on Neuroinformatics Research in
Vision through special coordination funds for promoting science and technology from the
Ministry of Education, Culture, Sports, Science and Technology (MEXT), and 13308048
from Japan Society for the Promotion of Science (JSPS), respectively.
References


Issa NP, Trepel C, and Stryker MP. Spatial frequency maps in cat visual cortex. *J Neurosci*


Figure Legends

Figure 1
Typical orientation and spatial frequency tunings are shown for a simple cell in area 17. Panels A and B show orientation and spatial frequency tuning curves obtained by drifting sinusoidal gratings. Error bars show standard errors. C shows a tuning surface in a joint orientation and spatial frequency domain obtained by a subspace mapping for the same neuron.

Figure 2
Comparisons are shown of tuning curves obtained by drifting gratings and subspace mappings. A shows a joint orientation and spatial frequency tuning surface for a complex cell in area 18. Dashed lines show the values of parameters used in the drifting grating tests. B shows orientation tuning curves obtained from tests using drifting gratings (solid curve) and from the subspace map (dashed curve). Similarly, C shows spatial frequency tuning curves obtained with drifting gratings (solid curve) and from the subspace map (dashed curve). Sample points are fitted with a Gaussian function. Error bars show the standard errors for the drifting grating data. D-F show another example of parameter comparisons for a complex cell in area 18.

Figure 3
Comparisons are shown of the optimal orientation and spatial frequency that are measured with the two methods. A compares the optimal orientation measured with drifting sinusoidal gratings (DSG), with that measured with subspace reverse correlation (SSRC). Pluses and open circles indicate data from areas 17 and 18, respectively. The solid line
shows linear regression and the dashed line indicates the exact match. 

**Figure 4**

Comparisons are shown of bandwidths for orientation and spatial frequency tunings measured with the two methods. 

- **A** shows comparisons of the half-width at half-height (HWHH) of orientation tunings. 
- **B** depicts the distribution of differences of the HWHH measured by the two methods, where a positive value indicates that the HWHH measured with the drifting gratings is greater than that from the subspace mapping. Similarly, **C** and **D** show comparisons of the spatial frequency bandwidth. The bandwidth of spatial frequency was defined as $\log_2(\frac{SF_{high}}{SF_{peak}})$, where $SF_{peak}$ is the optimal spatial frequency and $SF_{high}$ is the spatial frequency that falls to the half-maximum on the high spatial frequency side of the tuning curve obtained by Gaussian fit to the data.

**Figure 5**

Comparisons are shown of conventional F1/F0 ratio based on the drifting grating tests vs. modulation ratios estimated by the subspace mapping method (see text). 

- **A**, A joint distribution is shown of the F1/F0 ratios and modulation ratios obtained by the subspace mapping. Pluses and open circles indicate data from areas 17 and 18, respectively. 
- **B**, Correspondences of classifications into simple and complex cell
types are shown. Each bar shows the number of cells classified as a given type by the subspace reverse correlation (SSRC) out of a group classified by the drifting gratings (DSG). For example, C/C and S/S indicate the number of cells that are classified as complex and simple, respectively, using either method. And these dominate 205 (91%) of the all cells. Only 21 (9%) (C/S and S/C) cells were classified into different types by the two methods.

**Figure 6**
Refinement of selectivity map during the subspace mapping process is shown for a 2-d spatial frequency and orientation tuning for a complex cell in area 18. **A:** Each panel shows a selectivity map obtained by up to N-th iterations of stimulus presentations (e.g., the upper-left panel shows a selectivity map obtained from one iteration of stimulus presentation and the lower-right panel shows that from 15 iterations of stimulus presentation). The bottom panel shows a selectivity map obtained by all (in this case, 30 times) iterations of stimulus presentations. Response strengths are normalized by maximum values for each map. The number above each panel shows the correlation coefficient between the corresponding map and the final map. **B:** Growth of the correlation coefficients with time (see text) is shown. Error bars indicate the standard deviation.

**Figure 7**
Summary of the time course of refinement of selectivity maps is shown for all cells. **A** shows the growth of correlation coefficients for our sample of cells (N=371). The sample size is much larger than those for preceding figures, because only the subspace mapping data are needed. The dashed curve indicates the growth of correlation coefficients examined for random noise map, and the shaded area shows their SD. The time course and SD for the
Accuracy of subspace reverse correlation

random noise were average values of 50 times of simulations. B shows histograms of stimulation time necessary to attain a given accuracy criterion as defined by the correlation coefficient of 0.80, 0.90 and 0.95 (from top to bottom). The majority of cells reached the criterion of 0.8 within 2 minutes of stimulations. Even reaching the criterion of 0.95 required 5~10 minutes of stimulation time for the vast majority of neurons.

**Figure 8**

Temporal dynamics are shown of optimal orientation (A, C) and optimal spatial frequency (B, D) as obtained from subspace reverse correlation mapping. A shows temporal changes of optimal orientation over time course of responses. The duration of responses are defined as the range of correlation delays where SD of tunings exceed the mean + 5 SD of noise level. The response onset is the beginning of this duration. Horizontal dashed lines show the mean HWHH for orientation tunings (27.5 deg, from Fig. 4). C shows histogram for shifts of optimal orientation at 40 ms in A (dashed vertical line). B and D show the same for spatial frequency tunings. The mean HWHH for spatial frequency tunings were 0.56 octaves. There were no significant area dependencies in the distributions of shifts for both orientation and frequency tunings (Kolmogorov-Smirnov test, p>0.05). The number of cells shown in A and B is 352. For C, the numbers for areas 17 and 18 are 75 and 106, respectively. For D, the numbers for areas 17 and 18 are 89 and 110, respectively. The numbers of cells are smaller for C, D than A, B because the response durations are often shorter than 40 ms based on the S/N criterion.

**Figure 9**

Examples of spectro-temporal receptive fields (spatial frequency tunings at various correlation delays) are shown for two cells. A shows spatial frequency tunings obtained at
different correlation delays for a simple cell in area 18. Suppressive responses were represented as dashed contours. B and C show spatial frequency tuning curves obtained by drifting gratings (solid curve) and that from subspace mapping (dashed red curve). The tuning curve for the subspace mapping (red dashed curve) in B is based on the peak correlation delay, whereas that in C are derived as a sum of spatial frequency tuning at multiple correlation delays within the time range indicated by a red band at the top margin. A black marker in the band denotes the optimal correlation delay. Notations and format of the tuning curves are the same as in Figs. 2C and 2F. D shows data in the same format from a complex cell in area 17. This neuron exhibits a shift of optimal spatial frequency over the time course of the response. E, F: Match between the two testing methods is improved by integrating the spatial frequency tuning over multiple correlation delays as indicated by the red band at the top margin of panel D. G shows differences of bandwidth between estimations based on a single correlation delay and integrated tunings at multiple correlation delays. Each symbol indicates data from a cell. The result from multiple correlation delays is indicated by a symbol, circle or x, whereas that from a single correlation delay is shown by the endpoint of the corresponding tick. The style of symbol represents whether the differences are significant (circle) or not (x). Statistical significances were tested from 1000 times bootstrap re-samplings of frequency tunings for a single correlation delay, and judged by 95 percentile confidence intervals. Similar analyses are performed in H for estimations of differences of optimal spatial frequency. Data for the two examples above are pointed in G.

Figure 10
Correlations are shown for various tuning characteristics vs. differences of parameters obtained with the two methods. The correlation plots are shown in a matrix form. Each row
(and vertical axis) shows differences in estimated parameters between the two testing methods, from top row: optimal orientation, orientation bandwidth, optimal spatial frequency, and spatial frequency bandwidth. Each column (and horizontal axis) depicts a tuning characteristic that may affect the outcome, from left to right: direction selectivity, modulation ratio, signal-to-noise ratio (S/N), and peak firing rate. Each circle indicates a cell. The correlation coefficients and their p-values are indicated as insets in the plots, only for combinations that show significant correlations (p<0.05; test for Spearman’s correlation coefficient). The solid lines in the plots with significant correlations show linear regression.
Figure 1    Nishimoto, Arai and Ohzawa
Figure 2  Nishimoto, Arai and Ohzawa
Figure 4  Nishimoto, Arai and Ohzawa
Figure 5  Nishimoto, Arai and Ohzawa
Figure 6  Nishimoto, Arai and Ohzawa
Figure 7  Nishimoto, Arai and Ohzawa
Figure 8
Nishimoto, Arai and Ohzawa
Figure 9  Nishimoto, Arai and Ohzawa
Figure 10  
Nishimoto, Arai and Ohzawa