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Separable Cortical Maps Underlie Population Responses to Complex Visual Stimuli

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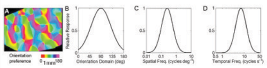
Abstract

In the earliest cortical stages of visual processing, a scene is represented in different functional domains selective for specific features. Maps of orientation and spatial frequency preference have been described in the primary visual cortex using simple sinusoidal grating stimuli. However, recent imaging experiments suggest that the maps of these two spatial parameters are not sufficient to describe patterns of activity in different orientation domains generated in response to complex, moving stimuli. A model of cortical organization is presented in which cortical temporal frequency tuning is superimposed on the maps of orientation and spatial frequency tuning. The maps of these three tuning properties are sufficient to describe the activity in orientation domains that have been measured in response to drifting complex images. The model also makes specific predictions about how moving images are represented in different spatial frequency domains. These results suggest that the tangential organization of primary visual cortex can be described as a set of separable receptive field feature maps including maps of orientation, spatial frequency and temporal frequency tuning properties.

Introduction

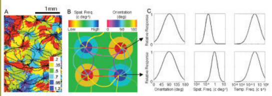
- In a recent experiment, Basole et al. (2003) showed that changing the temporal properties of a moving image can change which orientation domains are activated by the image.
- Their results suggested that the two spatial maps of cortical organization that have previously been proposed (orientation and spatial frequency) are not sufficient to describe the distributed responses of the cortex to moving images.
- We describe the functional organization of V1 in terms of the linear filters of the spatio-temporal energy model initially developed for individual neurons (Adelson and Bergen, 1985; Watson and Ahumada, 1985; Mante and Carandini, 2003, 2004).
- The separable cortical maps of orientaion, spatial frequency, and temporal frequency can describe the distributed responses of the cortex to complex moving stimuli.
- It is useful to consider cortical maps as maps of receptive field parameters rather than stimulus features. The average receptive field properties of a cortical domain determine the spatio-temporal tuning curves measured in response to drifting gratings.

The spatial and temporal organization of ferret area 17



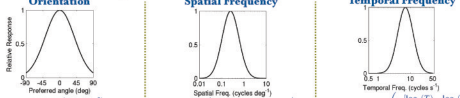
(orientation map modified from Issa et al., 1999)

The spatial and temporal organization of cat area 17



(orientation and spatial frequency map modified from Issa et al.,2000)

Population Tuning Curves: Spatio-temporal Filters



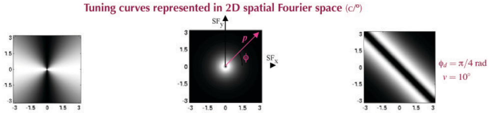
$$O(\tilde{\phi},\phi) = \exp\left(-\frac{[\phi-\tilde{\phi}]^2}{2\sigma_O^2}\right) \qquad S(p) = \exp\left(-\frac{[\log_2(p)-\log_2(S_p)]^2}{2\sigma_S^2}\right) \qquad T(v,\phi_d,p,\phi) = \exp\left(-\frac{[\log_2(T_i)-\log_2(T_p)]^2}{2\sigma_T^2}\right)$$

where $T_i = p\cdot v\cdot|\cos(\phi-\phi_d)|$

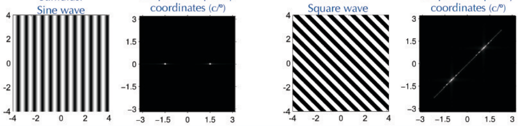
	Ferret area 17	Cat area 17
Orientation	$\tilde{\phi}$ varies point by point between 0 – 180°; $\sigma_O = 40°$ # §	
Spatial Frequency	$S_p = 0.25$ c/° †; $\sigma_S = 1.25$ c/° *	$S_p = 0.44$ c/° ‡; $\sigma_S = 1.63$ c/° ‡
Temporal Frequency	$T_p = 6-7$ c/s *; $\sigma_T = 0.8$ c/s *	$T_p = 2.23$ c/s ‡; $\sigma_T = 2.73$ c/s ‡

Parameters: # Rao *et al.*, 1997, † Baker *et al.*,1998, § Issa *et al.*, 1999, * estimated from fits to Basole *et al.*, 2003, ‡ Zhang and Issa, 2004

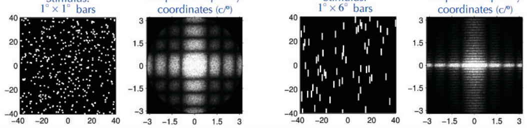
Tuning curves represented in 2D spatial Fourier space (c/°)



Visual Stimuli in Fourier Space

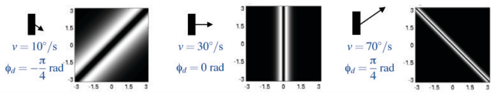


Effects of changing the aspect ratio



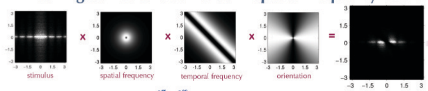
Effects of changing the drift angle & velocity

projection of the temporal frequency tuning curve onto spatial frequency coordinates



Population Response Model

Response in an orientation domain = integral of the product of all tuning curves and stimulus in spatial frequency coordinates



continuous: $$R(\tilde{\phi},v,\phi_d) = \int_{-\pi}^{\pi}\int_0^{\infty} A(p,\phi)\cdot S(p)\cdot T(v,\phi_d,p,\phi)\cdot O(\tilde{\phi},\phi)\; p\, dp\, d\phi$$

discrete: $$R(\tilde{\phi},v,\phi_d) = \sum_{i=1}^{N} A_i\cdot S_i\cdot T_i(v,\phi_d)\cdot O_i(\tilde{\phi})$$

$R(\tilde{\phi},v,\phi_d)$: response in the orientation domain $\tilde{\phi}$ to a textured stimulus drifting at an angle ϕ_d and velocity v

$A(p,\phi)$: amplitude of the Fourier Transform of the stimulus

$S(p)$: spatial frequency tuning curve

$T(v,\phi_d,p,\phi)$: temporal frequency tuning curve

$O(\tilde{\phi},\phi)$: orientation tuning curve peaked at $\tilde{\phi}$

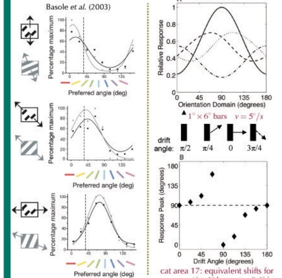
Model Predictions

Drift Angle

changing drift angle changes the orientation domains activated

Experiment: ferret area 17, Basole *et al.* (2003)

Model Results: ferret area 17



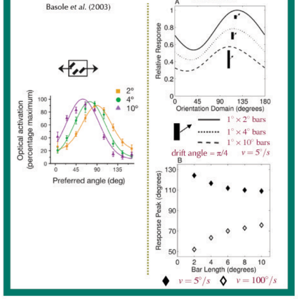
cat area 17: equivalent shifts for 1° × 2° bars; $v = 0.6°/s$

Aspect Ratio

changing bar length reduces the effect of different drift angles

Experiment: ferret area 17, Basole *et al.* (2003)

Model Results: ferret area 17

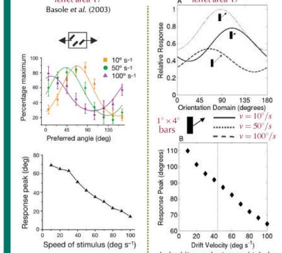


Drift Speed

changing drift velocity shifts the preferred orientation

Experiment: ferret area 17, Basole *et al.* (2003)

Model Results: ferret area 17



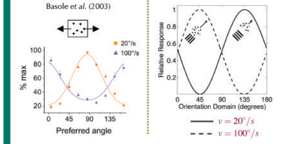
dashed line: velocity at which the peak population response matches the orientation of the bars of the stimulus (ferret: $v = 44°/s$; cat: $v = 10.5°/s$)

Random Dot Motion

abrupt transitions between orientation domains activated as drift velocity is increased

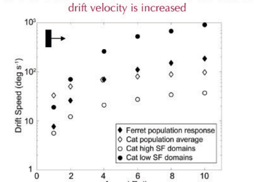
Experiment: ferret area 17, Basole *et al.* (2003)

Model Results: ferret area 17



Abrupt Shifts with Orthogonal Motion

transitions between orientation domains activated as drift velocity is increased



drift velocity at which population response shifts by 90° degrees

Psychophysics: Above a threshold speed, motion streaks are perceived along the direction of motion of an image (Geisler, 1999; Geisler *et al.*, 2001)

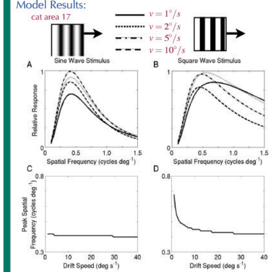
Shifts in Spatial Frequency Domains

changing drift velocity shifts the preferred spatial frequency

Model: Response in a domain with spatial frequency preference $\tilde{p}$

$$R(\tilde{p},v,\phi_d) = \int_{-\pi}^{\pi}\int_0^{\infty} A(p,\phi)\cdot S(\tilde{p},p)\cdot T(v,\phi_d,p,\phi)\cdot O(\phi)\; p\, dp d\phi$$

Model Results: cat area 17



Psychophysics: Visual acuity changes with image speed (dynamic acuity; Levi, 1996.)

Experiment: Zhang and Issa, 2004

Conclusion

- The organization of V1 can be characterized by separable receptive field feature maps of 6 tuning parameters.
- The spatio-temporal energy description of V1 can be reconciled with the current description of spatial maps (orientation & spatial frequency preference) by superimposing temporal frequency tuning.
- The model predicts transitions in the responses of different orientation domains seen in experiments (Basole et al., 2003.)
- The model predicts the 90° flip in peak orientation response for textures moving orthogonally past a transition velocity, consistent with the perception of motion streaks.
- The model predicts transitions in the responses of different spatial frequency domains that might underlie dynamic visual acuity.
- The model only describes the linear component of responses in V1 – nonlinearities can be extracted by comparison to actual responses (e.g. see Zhang and Issa, poster 648.6.)

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