Engineering-approach accelerates computational understanding of V1–V2 neural properties

Shunji Satoh · Shiro Usui

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Abstract We present two computational models (i) long-range horizontal connections and the nonlinear effect in V1 and (ii) the filling-in process at the blind spot. Both models are obtained deductively from standard regularization theory to show that physiological evidence of V1 and V2 neural properties is essential for efficient image processing. We stress that the engineering approach should be imported to understand visual systems computationally, even though this approach usually ignores physiological evidence and the target is neither neurons nor the brain.

Keywords V1 · V2 · Long-range horizontal connection · Filling-in · Blind-spot

Introduction

Neuroscience will contribute to construction of novel algorithms and architectures to solve current problems related to image processing because the visual system is the ultimate system for effective image processing.

To understand visual functions, three levels of analysis are important (Marr 1983):

- what problems vision solves and why (computational level)
- strategies that might be used in the visual system (algorithmic level), and I/O representation (representational level)

- how strategies are executed in the neural activity (implementational level)

Neurophysiology, computational neuroscience, and psychophysics are natural approaches to explore those three levels.

From an engineering point of view, we can regard the visual system as a large-scale machine for image processing or as a collection of many algorithms to solve various problems. Myriad new problems and computer algorithms have been presented from an engineering perspective and proposed independently of brain science.

These engineering studies rarely consider neurophysiological evidence. However, such studies actually contribute to vision science because their efforts are also aimed at finding problems to be solved (computation) and the effective methods used to solve them (algorithms). Implementation levels are different, but the computation level and the algorithmic level are the same as those of vision science. For that reason, neurophysiologists and computational neuroscientists can find many clues to explain complicated visual properties from studies that are unrelated to brain science.

Meanwhile, vision scientists already have novel ideas to construct effective image processing algorithms because they know some algorithms of *existing* biological highly efficient machines for image processing (=visual system). Therefore, we expect that neurophysiology, computational neuroscience, and psychophysiology are matrices of efficient image processing.

In this article, two examples of computational visual model are introduced based on standard regularization theory (SRT) (Poggio et al. 1985). The SRT is a powerful tool to understand the visual system computationally (scientific contribution) and to develop effective image

S. Satoh (✉) · S. Usui
Laboratory for Neuroinformatics, RIKEN Brain Science
Institute, Hirosawa 2-1, Wako, Saitama 351-0198, Japan
e-mail: shun@brain.riken.jp

processing methods (engineering contribution). The first target of this article is the long-range horizontal connections in V1; the second target is the filling-in process and neural properties of the blind spot.

Standard regularization theory

A short overview of standard regularization theory (SRT) is presented. The advantages of SRT are (i) computational models derived from SRT can be regarded as *optimizers* of evaluation functions, and (ii) numerous algorithms for image analysis based on the optimization process have been presented from engineering perspectives.

Equation 1 is an example of evaluation functions for image reconstruction. We will show that long-range horizontal connections in V1 are necessary to execute image reconstruction by neural circuits, and a model for filling-in process at the blind spot is also derived from Eq. 1.

$$E[I(t)] = \underbrace{\frac{\alpha}{2} \int d^2\mathbf{x} (I(\mathbf{x}, t) - J(\mathbf{x}))^2}_{E_{\text{fit}}[I]} + \underbrace{\frac{\lambda}{2} \int d^2\mathbf{x} \|\nabla I(\mathbf{x}, t)\|^2}_{E_{\text{reg}}[I]}, \quad (1)$$

where $J(\mathbf{x})$ represents the luminance of an observed image that is contaminated by noise at a spatial position $\mathbf{x} = (x, y) \in \mathbb{R}^2$, and $I(\mathbf{x}, t)$ represents a reconstructed image at time t . Therein, α and λ are positive constant parameters. Usually, the restriction of $\alpha/2 + \lambda/2 = 1$ is reasonable because the error and the regularization term, E_{fit} and E_{reg} , are trade-off, but we consider general cases for those coefficients in this article (e.g. λ will be a mathematical function). Hereafter, we assume $\alpha = 1$ and $x = \mathbf{x} \in \mathbb{R}$ in this section for simple discussion. Image reconstruction involves the inference of an original (unknown) image I from J . The $E[I(t)]$ is designed so that it takes a smaller value when I is a desired image. The dynamics of I can be derived by applying the steepest descent method to the functional $E[I(t)]$:

$$\tau \frac{\partial}{\partial t} I(x, t) = J(x) - I(x, t) + \lambda \frac{\partial^2}{\partial x^2} I(x, t), \quad (2)$$

where τ is a time constant. Hereafter, we assume $\tau = 1$ for simple discussion. The steady state of $I(x, t)$ is the result of reconstruction.

We assume here that V1 cells have dedicated operation not only to edge-detection, but also to image reconstruction. The output of such a V1 neuron is designated as s_θ , which is selective to θ -oriented edges. We can obtain the dynamics of s_θ from Eq. 2 deductively, as

$$\tau \frac{\partial}{\partial t} s_\theta(x, t) = g_\theta * \left(\tau \frac{\partial}{\partial t} I(x, t) \right), \quad (3)$$

Fig. 1 **a** Neural implementation of image reconstruction with single spatial resolution. **b** Image processing using multi-resolution method with different discretization steps

$$= g_\theta * J(x) - s_\theta(x, t) + \lambda \frac{\partial^2}{\partial x^2} s_\theta(x, t), \quad (4)$$

where $*$ is the spatial convolution and g_θ is the Gaussian derivative function, which is similar to a Gabor function, representing the spatial distribution of the receptive field (RF) (Young et al. 2001). The positional variable x signifies the retinal position of the RF center. The parameter $\lambda > 0$ is identical with one of Eq. 1, and the λ is the diffusion constant of the (forward-)diffusion process of s_θ .

A neural network for edge-detection and image reconstruction is obtained by discretizing the positional variable x of Eq. 4. One example is the following.

$$\tau \frac{\partial}{\partial t} s_\theta(x, t) = g_\theta * J(x) - (1 + \lambda) s_\theta(x, t) + \lambda (s_\theta(x-1, t) + s_\theta(x+1, t)) \quad (5)$$

The first term of the right-hand-side of Eq. 5 represents a masking operation to detect θ -oriented edges in a retinal image J . Figure 1a is a schematic diagram representing neural implementation of the second and third terms of Eq. 5. Since we find self-inhibition $(1 + \lambda)$ and an excitatory intra-cortical (lateral or horizontal) effect λ , we expect that such lateral effect is a neural implementation to optimize (minimize) a pre-defined function $E[I(t)]$ for image reconstruction.

Long-range horizontal connections

Neural evidence

We here consider the intra-cortical (horizontal) effect between V1 neurons, conveyed through long-range horizontal connections (LHCs). As shown in Fig. 2a, the LHCs in V1 tend to link orientation-selective cells with similar orientation preferences (Bosking et al. 1997; Rockland and Lund 1982). This preference is described as iso-orientation connectivity.

The horizontal effect is very complicated as follows. As shown in Fig. 2b, changing the stimulus intensity to the

Fig. 2 **a** and **b** The average number of boutons of long-range horizontal connections and nonlinearity of lateral effects. (adapted from Bosking et al. (1997), Weliky et al. (1995)) **c** and **d** Simulation results

pre-synaptic cell alters the balance of the evoked post-synaptic excitation and inhibition without changing the iso-orientation connectivity of the horizontal connections (Weliky et al. 1995). Figure 2b shows polarity changes in excitatory and inhibitory post-synaptic currents (PSCs) of a V1 (layers II/III) cell as a function of the stimulus intensity provided to pre-synaptic cells. The recording cell showed excitation when a low-amplitude stimulus was provided to pre-synaptic cells, but an inhibitory effect was dominant with a higher-amplitude stimulus. We intend to answer the following questions:

- What is the computational theory of LHCs?
- What is the advantage of the polarity change for image processing?

Computational theory and algorithm

We investigate the computational necessity of polarity change of horizontal effects from an engineering point of view.

As shown in Fig. 1a, horizontal effect is formulated by $\lambda s_\theta(x \pm 1)$. Polarity change implies that λ , which is a diffusion coefficient, is not constant, but it can be a positive or a negative value depending on the value of $s_\theta(x \pm 1)$. In other words, the diffusion process of s_θ is forward-diffusion when $\lambda > 0$, and backward-diffusion when $\lambda < 0$.

We can find a candidate of the computational theory and algorithm from an engineering perspective. Perona and Malik (1990) have proposed an efficient algorithm for image reconstruction using a context-dependent ($J(x)$ -dependent) diffusion-coefficient. A lot of algorithms for image reconstruction have been proposed based on the Perona–Malik algorithm (Black et al. 1998; Gilboa et al. 2002). Therefore, we expect that the computational theory of LHCs should be image reconstruction and the algorithm should be the forward-diffusion and backward-diffusion processes.

Based on the Perona–Malik functional (evaluation function), the following functional is a strong candidate of the evaluation function to understand the computational theory of LHCs from an engineering perspective.

$$E_H[I(t)] = E_{\text{fit}}[I] + \frac{1}{2} \int d^2x d\rho \Lambda \left(\frac{\partial}{\partial \rho} J(x) \right) \left\{ \frac{\partial}{\partial \rho} I(x, t) \right\}^2 \quad (6)$$

In the equation, $\partial/\partial \rho$ is the directional derivative in the direction of ρ . The function $\Lambda(a) = (\lambda/k)/(1 + (a/k)^2)$ is referred to as an edge-function (Perona and Malik 1990).

Moreover, multi-resolution method is introduced into Eq. 6 to represent the “long-range” property of LHCs. As shown in Fig. 1b, “long-range” implies multiple spatial resolutions of spatial discretization. The multi-resolution method is realized using Gaussian blur for J and I . We therefore obtain

$$E_H[I(t)] = E_{\text{fit}}[I] + \frac{1}{2} \int d^2x d\rho \int d\sigma \Lambda \left(\frac{\partial}{\partial \rho} J_\sigma(\mathbf{x}) \right) \left\{ \frac{\partial}{\partial \rho} I_\sigma(\mathbf{x}, t) \right\}^2, \quad (7)$$

where $J_\sigma(\mathbf{x}) = \sigma \{g_\sigma * J(\mathbf{x})\}$, $I_\sigma(\mathbf{x}, t) = \sigma \{g_\sigma * I(\mathbf{x}, t)\}$ and g_σ is the two-dimensional Gaussian function with σ^2 variance.

Assuming $J \simeq I$, we obtain the dynamics of orientation-selective neurons, which devote their operation not only to edge-detection but also to image reconstruction using multi-resolution method:

$$\frac{\partial}{\partial t} s_\theta(\mathbf{x}, t) = g_\theta * J(\mathbf{x}) - s_\theta(\mathbf{x}, t) + \int d\rho \int d^2x' W_{\theta\rho}(\mathbf{x}') \psi(s_\rho(\mathbf{x} - \mathbf{x}', t)), \quad (8)$$

$$W_{\theta\rho}(\mathbf{x}') = \int d\sigma \sigma^2 \frac{\partial^2}{\partial \rho \partial \theta} g_\sigma(\mathbf{x}'), \quad (9)$$

$$\psi(s_\rho) = \lambda \frac{(s_\rho/k) - (s_\rho/k)^3}{(1 + (s_\rho/k)^2)^2}.$$

We obtained Eq. 8 by applying the steepest descent method to Eq. 7, and by using Eq. 3. Equation 8 means that $s_\theta(\mathbf{x}, t)$ is affected by other V1 neurons $s_\rho(\mathbf{x} - \mathbf{x}', t)$ with long-range connections signified by $W_{\theta\rho}(\mathbf{x}')$; the lateral effect is a nonlinear function $\psi(s_\rho)$.

Simulation

We find the computational W and ψ are consistent with physiological evidence shown in Fig. 2a and b. Figure 2c presents the plot of connection strength $W_{\theta\rho}$ as the function of orientation difference $\theta - \rho$.¹ Figure 2d shows the physiological nonlinearity of the horizontal effect (total PSC = EPSC – IPSC : $\square = \bigcirc - \blacksquare$) and the computational nonlinearity $\psi(s^\eta)$ when $\eta = \theta$.

Figure 3 shows simulation results of Eq. 8. We find the efficiency of the computational model. Figure 3a is an input (retinal) image J contaminated by noise. Its size is 128×128 pixels and its luminance is normalized so that $0 \leq J \leq 1$. Parameters are $\lambda = 0.1$, $k = 0.07$, ρ and $\theta \in \{0, \pi/4, \pi/2, 3\pi/2\}$ (four orientations). The number of simulated V1 neurons is $4 \times 128 \times 128$. Figure 3b depicts the initial outputs of $s_\theta(\mathbf{x}, t)$. A short line segment at each position x represents the orientation of the maximally reacting neuron among the four neurons. Figure 3c depicts the steady state of $s_\theta(\mathbf{x}, t)$. As time progresses, noise is

suppressed; continuous curves are enhanced and integrated because the model neurons perform image reconstruction.

Discussion

The contribution of the previous section is summarized as the following:

Scientific contribution We can understand the polarity change and LHCs as a neural implementation of the forward-backward diffusion method and the multi-resolution method for image reconstruction.

Engineering contribution We propose a new algorithm for edge-detection using multi-resolution and forward-backward diffusion.

We see a limitation of our computational model for horizontal connections in Fig. 3c: noise is suppressed, but the positional uncertainty of detected edges is large. The model cannot determine the correct edge positions because the detected edges in Fig. 3c distribute over three or four pixel width. This poor positional certainty is due to the Gaussian kernels g_σ . The Gaussian kernels are necessary to represent “long-range” property of connections, but coarser spatial resolution with large variances (large σ) results in spatial blurring operation for images. To solve this problem, other neural circuits, e.g. short-range horizontal connections, feed-back information from higher order cortices and the nonlinear temporal interactions between axonal spikes (Haken 2007) will be required.

While the proposed model reproduces the mean of the connection data (Fig. 2c) with some agreement, it does not reproduce the individual connection patterns implied by error bars in Fig. 2a. Such diverse connection patterns would be obtained by considering the various shape of V1 receptive fields (Ringach 2002).

Filling-in at the blind spot

Neural evidence

We next specifically examine the filling-in process at the blind spot (BS). The BS is the area of the visual field that corresponds to the lack of photoreceptors because of the optic disk. We do not see any black disks or strange patterns in our visual fields; rather, we perceive the colors or patterns surrounding the BS. This phenomenon is referred to as perceptual filling-in at the BS.

Komatsu and colleagues reported a quantitative analysis of V1 neural responses of awake macaque monkeys to bar stimuli presented on the blind spot (Komatsu et al. 2000; Matsumoto and Komatsu 2005). The receptive fields (RFs) of the recorded neurons overlapped with the BS area

¹ $W_{\theta\rho}(\mathbf{x}')$ is decomposed into two Gaussian functions: $G_{\theta\rho}^{\text{exc}}(\mathbf{x}') - G_{\theta\rho}^{\text{inh}}(\mathbf{x}')$, also known as the DoG function. Figure 2c is a plot of $\int d\mathbf{x}' \{G_{\theta\rho}^{\text{exc}}(\mathbf{x}') + G_{\theta\rho}^{\text{inh}}(\mathbf{x}')\}$.

Fig. 3 **a** Input pattern. **b** Initial output of orientation selective neurons. **c** Steady state

Fig. 4 **a** Schematic examples of bar stimuli. **b** Retinal inputs. **c** Responses of the recorded neuron. (adapted from Matsumoto and Komatsu (2005)). **d** Simulation result

(Fig. 4a). Bar stimuli of various lengths were present at the BS. One end of the bar stimulus was fixed; the other end was varied (Fig. 4(a1)–(a4)). Some V1 neurons showed a marked increase in their activities when the bar end exceeded the BS (Fig. 4c), whereas those activities remained constant as long as the end was inside of the BS area. These results indicate that V1 neurons perform filling-in processes as well as orientation detection.

Moreover, Matsumoto and Komatsu conjectured the existence of two different pathways with different velocities of visual signals: (i) fast feedforward and fast feedback connections, such as $V1 \rightarrow V2 \rightarrow V1$; and (ii) slow intra-cortical connections linking V1 neurons, such as $V1 \rightarrow V1$. Then, we discuss the computational necessities:

- Why are V2 neurons required for V1 filling-in?
- Why are the different velocities necessary for filling-in?

Computational theory and algorithm

As shown in Fig. 5a, the BS area and the boundary are respectively referred to as $\mathcal{B}$ and $\partial\mathcal{B}$. One purpose is to obtain a filled-in pattern like that depicted in Fig. 5b from the initial condition of Fig. 5a.

We consider an appropriate evaluation function for the filling-in process to obtain the desired filled-in pattern. Considering the lack of input in the BS ($\alpha = 0$ of Eq. 1), it

is apparent that E_{BS} defined in Eq. 10 is a simple evaluation function based on Eq. 1.

$$E_{BS}[I(t)] = E_{reg}[I] = \frac{\lambda}{2} \int_{\mathcal{B}} d^2\mathbf{x} \|\nabla I(\mathbf{x}, t)\|^2. \quad (10)$$

Unfortunately, the filled-in pattern minimizing the above E_{BS} is not a completed bar, but fragmented bars, as shown in Fig. 5c.

To obtain a completed bar as a result of filling-in, Eq. 10 is modified by introducing physiological evidence: V2 neurons are required for V1 filling-in. Some V2 neurons are selective to angles embedded within V-shaped patterns composed of oriented line segments (Ito and Komatsu 2004). We therefore introduce two kinds of angular information of oriented lines, $\bar{\kappa}$ (curvature of level-set) and $\bar{\mu}$ (curvature of flow-line), into Eq. 10.

$$E_{BS}[I(t)] = \frac{1}{2} \int_{\mathcal{B}} d^2\mathbf{x} \{ \bar{\kappa}^2(\mathbf{x}, t) + \bar{\mu}^2(\mathbf{x}, t) \} \|\nabla I(\mathbf{x}, t)\|^2, \quad (11)$$

where

$$\bar{\kappa} = \frac{I_y^2 I_{xx} - 2I_x I_y I_{xy} + I_x^2 I_{yy}}{I_x^2 + I_y^2},$$

$$\bar{\mu} = \frac{(I_x^2 - I_y^2) I_{xy} - I_x I_y (I_{yy} - I_{xx})}{I_x^2 + I_y^2}, \quad (12)$$

where subscripts of I represent partial derivatives. Note that λ of Eq. 10 has been replaced by $\bar{\kappa}^2 + \bar{\mu}^2$ in Eq. 11. The curvatures of equi-luminance contours (level-sets) of an

Fig. 5 **a** Filling-in process is applied in BS area $\mathcal{B}$ (a gray rectangle). **b** Example of a desired filling-in pattern. **c** Filling-in using the diffusion equation. **d** Filling-in using the proposed visual model

image I are evaluated using $\bar{\kappa}$. The curvatures of flow lines, which are perpendicular to level-sets, are evaluated using $\bar{\mu}$. See Fig. 6 for examples of level-sets and flow curves. Smaller values of $\bar{\kappa}^2$ and $\bar{\mu}^2$ represent more continuous contours of a filled-in pattern.

We can rewrite Eq. 11 using local coordinate systems (η, ξ) exemplified in Fig. 6. The direction ξ is parallel to the gradient direction ∇I , and η is perpendicular with ξ . Note that $\|\nabla I\| = (\partial/\partial\xi)I$, where $(\partial/\partial\xi)$ is the directional derivative in the direction of ξ . Similarly, $\bar{\kappa} = (\partial^2/\partial\eta^2)I$, and $\bar{\mu} = (\partial^2/\partial\eta\partial\xi)I$ (Kanatani 1990; Lindeberg 1994). We obtain

$$E_{BS}[I(t)] = \frac{1}{2} \int_{\mathcal{B}} d^2\mathbf{x} \left\{ \left(\frac{\partial^2}{\partial\eta^2} I(\mathbf{x}, t) \right)^2 + \left(\frac{\partial^2}{\partial\eta\partial\xi} I(\mathbf{x}, t) \right)^2 \right\} + \left(\frac{\partial}{\partial\xi} I(\mathbf{x}, t) \right)^2. \quad (13)$$

Equation 13 indicates that E_{BS} consists of the first and the second order derivative image features.

We expect that the dynamics for filling-in can be obtained deductively by applying the steepest descent method to Eqs. 11 or 13. The following equation shows the resultant complex dynamics.

Fig. 6 An example of locally defined coordinate system (η, ξ) . Different gray levels represent different luminance of an image. Level-sets are equi-luminance contours, and flow lines are perpendicular to level-sets. In the (η, ξ) coordinate system, the ξ -direction is at every point parallel to the gradient direction of I , and the η -direction is parallel to the flow-curve (parallel to the tangent to the level-set)

$$\begin{aligned} \frac{\partial}{\partial t} I = & (I_y^6 I_{yyyy} I_x^2 + 3I_y^4 I_{yyyy} I_x^4 + 3I_y^2 I_{yyyy} I_x^6 \\ & + \dots (74 \text{ terms}) + \dots \\ & + 3I_y^6 I_x^4 I_{xxxx} + 3I_y^4 I_x^6 I_{xxxx} + I_y^2 I_x^6 I_{xxxx}) / (I_x^2 + I_y^2)^{3/2} \end{aligned} \quad (14)$$

The problematic complex equation, Eq. 14, includes 80 terms. It seems impossible to analyze all 80 terms to investigate their physiological meanings.

We again try to use a physiological phenomenon as a key to solving the problem. The key is the different pathways with different conductance velocities: *fast pathways via V2, and slow pathways within V1* (horizontal connections). The faster conductance velocity of the visual pathway via V2 implies the faster optimization of $\bar{\kappa}(\mathbf{x}, t)$ and $\bar{\mu}(\mathbf{x}, t)$ in time than that of $\|\nabla I(\mathbf{x}, t)\|$. In an extreme situation of the velocity difference, we can assume a constant value of $\|\nabla I(\mathbf{x}, t)\|$ with respect to time t . This assumption corresponds to variable separation and adiabatic approximation. Applying the steepest descent method to Eq. 11 using this assumption, we obtain the following dynamics.

$$\frac{\partial}{\partial t} I(\mathbf{x}, t) = \left(\frac{\partial}{\partial\eta} \bar{\kappa} + \frac{\partial}{\partial\xi} \bar{\mu} \right) - \left(\frac{\partial^2}{\partial\xi^2} + \frac{\partial^2}{\partial\eta^2} \right) \bar{\kappa} + \beta I_{\eta\eta}, \quad (15)$$

Therein, $\bar{\kappa} = I_\xi^2 \bar{\kappa}$, $\bar{\mu} = I_\xi^2 \bar{\mu}$ and β is a positive constant. The fourth term of Eq. 15 is a consistency term, which alleviates the drawbacks of variable separation and adiabatic approximation. Comparing with Eq. 14, we find a simple, analyzable, neural implementable equation in Eq. 15.

Simulation

First, numerical simulations of Eq. 15 are performed to investigate whether the expected filling-in pattern is obtained using Fig. 5a as the initial value of I . A parameter is $\beta = 0.1$. Figure 5d is the steady state of I (filling-in pattern). We find an expected pattern of Fig. 5d, in which a broken bar of Fig. 5a is completed.

We evaluate the efficiency of our visual model in a more difficult situation of recovering a damaged image. The results are portrayed in Fig. 7, in which the region $\mathcal{B}$ is a checkered orange area (Color results might be available on

Fig. 7 **a** Almost half of visual information is missing. **b** Restored image using the proposed visual model

the electric version of this article). We find a high ability to recover missing information in our visual model.

Finally, we simulate the physiological experiments shown in Fig. 4. The dynamics of V1 neurons in the BS region is obtained by substituting Eq. 15 into Eq. 3. Figure 4d illustrates the steady values of s_θ for various lengths of input bars. We find consistency between physiological results and our model.

Discussion

The contribution of the previous section is summarized as the following:

Scientific contribution V2-coding information (angles embedded within V-shaped patterns) is necessary to represent the continuity of desired filled-in patterns at the BS region. Moreover, different conductance velocities are useful for simple and effective dynamics for filling-in.

Engineering contribution Novel dynamics for image inpainting (recovering missing information) can be proposed using computational vision science.

A drawback of our filling-in model is that any textures cannot be recovered because the evaluation function E_{BS} only evaluates continuity of luminance (DC component of images), and it does not evaluate spatial continuity of texture features. One way to solve the problem will be to introducing higher order (more than third order) derivative features of images E_{BS} .

Summary

We have shown that many areas of study, which are apparently unrelated to brain science, are important to understand visual systems computationally. We hope that physiologists and computational vision scientists export

their knowledge to construct novel algorithms for effective image processing, and that they adopt an import engineering-oriented approach to understand neural evidence as neural implementations of image processing.

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