

Discriminative responses of squid (*Loligo pealeii*) photoreceptors to polarized light

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Abstract

Cephalopods behaviorally respond to polarized light. Electrophysiology experiments with the squid, *Loligo pealeii*, demonstrated that spike responses from individual photoreceptors are a cosine² function of the e-vector orientation of a polarized stimulus. The discrimination limit to this polarization sensitivity depended upon the difference between the orientation of a polarized stimulus with a preferred e-vector. The limit ranged from 2° to 9.2° with a direct stimulus in the dark or 4.8°–22.1° with non-directed background illumination and the cells were least discriminative at the preferred orientations. This limit can be explained partly by the variability in anatomical alignment of microvilli in the photoreceptors around a dominant axis. A few light-sensitive retinal fibers showed no polarization sensitivity. The coding of polarization information suggests that light intensity is transformed into an average spike rate. This average results from silent periods interspersed between bursts of spikes, each burst possessing a consistent interspike interval. The variations in the length and frequency of silent periods depend upon the difference between the polarization e-vector and a preferred e-vector orientation. The minimal discriminated orientation of a squid photoreceptor agrees well with the minimum behavioral discrimination of polarized light by another cephalopod, the octopus.

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1. Introduction

Despite the remarkable visual behavior of cephalopods, the relationship between visual behavior and the neural operations of visual processing remains at a primitive understanding relative to other visually dependant taxa, eg., the vertebrata, insecta, and crustacea. Studies have revealed many aspects of cephalopod visual structures, including photoreceptor structure (Zonana, 1961; Yamamoto et al., 1965; Cohen, 1973a,b; Saibil, 1982; Robles et al., 1984), biochemistry of photoreception (Hara and Hara, 1972; Roffe, 1975; Messenger, 1977, 1991; Muntz, 1986; Saibil,

1990a; Michinomae et al., 1994), cellular neurophysiology of photoreceptors (including the photoreceptor potential, Hagins, 1965; Duncan and Weeks, 1973; Pinto and Brown, 1977; Duncan and Pynsent, 1979), and ERG responses of the retina (Duncan and Weeks, 1973; Messenger, 1991), and also limited aspects of the dynamics of photoreceptor spiking (Hartline and Lange, 1974; Lange and Hartline, 1974; Tasaki et al., 1974; Orlov et al., 1981; Saidel et al., 1983). In addition, the neuroanatomy of the visual nervous system has been studied in detail (Young, 1960, 1962a,b, 1974). Despite the classification of photoreceptors as ‘on’, ‘on–off’, and ‘off’ or as ‘slow’ or ‘fast’, remarkably little is known about the relationship between visual physiology, information processing and visually guided behavior except that retinal information, conveyed by a spike train (MacNichol and Love, 1960; Lange and Hartline, 1974;

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Saidel et al., 1983) is conducted by axons of photoreceptors that terminate in the optic lobe periphery or ‘retina profunda’ (Young, 1962a,b).

In one particular area, i.e., response to polarized light, progress has been made connecting neural processing with its behavioral relevance. Polarization sensitivity has long been recognized as a major aspect of cephalopod visual behavior (Moody and Parriss, 1960; Rowell and Wells, 1961; Jander et al., 1963; Shashar and Cronin, 1996; Shashar et al., 1998, 2002). Physiologically, the ERG in octopus (Tasaki and Karita, 1966) and the receptor potential of a photoreceptor (Sugawara et al., 1971) respond to the plane of polarization as does the rate of spike firing by individual squid photoreceptors (Lettvin and Maturana, 1962; Saidel et al., 1983). The orientation or plane of maximal polarization sensitivity – a “preferred plane” – may be defined physiologically for a cephalopod photoreceptor. Discrimination of linearly polarized light is also common at the initial stages of the visual pathway of other invertebrate microvillar-based visual systems, e.g., butterfly (Bandai et al., 1992), crab (Waterman and Horch, 1966), cricket (Labhart, 1988; Labhart and Petzold, 1993; Blum and Labhart, 2000), desert ants (Labhart, 2000), and waterstrider (Bartsch, 1995).

The anatomy and physiology of photoreceptors restrict polarization sensitivity and the detection threshold for changes in the e-vector orientation of polarization relative to a preferred orientation (Goldsmith, 1977; Nilsson et al., 1987). Numerous intrinsic factors potentially might affect the response of a rhabdomeric photoreceptor to a polarized stimulus including: (i) the length and width of the microvilli, (ii) the arrangement and density of the retinal molecules within the microvillar membrane, (iii) the length of the photoreceptor as compared to light availability, (iv) the existence of scattering pigments or other scattering structures within the light path, and (v) the alignment of the microvilli within a photoreceptor.

The microvilli of the polarization-sensitive photoreceptors in the dorsal rim of the eyes of desert ants and crickets are highly aligned along the radial length of their photoreceptors (Nilsson et al., 1987). In squid, most neighboring photoreceptors vary not more than 10° from orthogonality (with a small percentage of receptors varying from neighbors by 45° ; Shashar et al., 2002). Since viewing a small target – such as a small prey – involves a limited number of photoreceptors in a restricted region of the retina, approximately half the photoreceptors seeing a target will have a preferred plane of polarized light roughly orthogonal to the other half of this photoreceptor population.

Two sources of irregularity could reduce an animal’s ability to detect partial polarization and impair its angular discrimination ability in polarization space. One is a previously identified irregularity of $\sim 10^\circ$ in microvillar orientation across cells (Shashar et al., 2002). The other is

variation of a photoreceptor’s microvilli orientations within its outer segment. In the present paper, we studied single photoreceptor’s responses to different orientations of polarization and we also determined the variation of a receptor’s microvilli orientations. In so doing, we directly asked about the origin of behavioral limitations to a cephalopod’s detection of changes in the e-vector orientation of polarized light?

2. Methods

Electrophysiological responses from individual photoreceptors were obtained following the isolated eye procedure (Hartline and Lange, 1974; Lange and Hartline, 1974; Saidel et al., 1983). Freshly isolated eyes from the squid *Loligo pealeii* were quickly dissected in a petri dish filled with chilled, oxygenated seawater positioned within a well of ice. After isolating the eye, the muscle surrounding the optic nerves was quickly removed to increase oxygenation of the retinal fibers. (We emphasize here that speed is of the essence. The most successful preparations were those that were mounted within two minutes from excision. Spike responses were rarely obtained in preparations that took longer than 5 min to prepare.) The eye was next mounted on a plastic holder, such that it was positioned centrally within a hole in the mount, and the mount placed in a chamber equipped with a thin hemispherical glass window (modified after a design of Lange and Hartline, 1974). The eye was positioned at the center of the globe facing the glass hemisphere. The chamber was filled with chilled, oxygenated seawater, which was constantly replaced via a standard medical I.V. drip connector. The sclera covering the optic nerves as they course along the back of the eye was excised, taking care not to stretch the nerve fibers lying beneath. Membranes overlying the optic nerves were removed and the proximal ends of exposed retinal nerve fibers were pulled into a suction electrode of diameter $<30\ \mu\text{m}$ with gentle suction. The electrophysiological signals from one or a few photoreceptor axons were obtained from these exposed nerve fibers. Signals were amplified, filtered (Axon AxoClamp 2B or Grass P15 in combination with an Axon CyberAmp 320), audio-monitored (Grass AM 8) and displayed with an oscilloscope. The signals were simultaneously A/D sampled with an Axon system (Axon Digidata 1320A) and with a program designed in Capital Equipment Corporation’s Test Point environment, and displayed and stored on computers for post-experimental analysis. The preparation was illuminated with a Schott KL 1500 controlled tungsten lamp via a fiber optic mounted in a custom-made rotatable arm that maintained the fiber optic illumination radial to the eye at all times (using a design provided by Dr. R. Barlow, Syracuse University). The light passed through a diffuser followed by a rotatable

linear polarizer (Polaroid HNP'B) placed at the end of the fiber optic. A Uniblitz electronic light shutter controlled the duration of light exposure. All procedures were performed in the dark and the eyes were dark-adapted for at least 30 min before initial measurements.

We obtained data from photoreceptors that, when stimulated near the middle of their operating range, could generate spike trains (see results). At the low end of a photoreceptor's dynamic range, only a few spikes are produced despite a stimulus near the preferred plane of polarization, while at the high end of its dynamic range, a photoreceptor may saturate as demonstrated by complete spike suppression (Lange and Hartline, 1974; Saidel et al., 1983). Data files were processed off-line using Test Point software. Recordings were made from 14 light-sensitive cells. For the most detailed analysis, we used data from 7 cells in which responses could be elicited over the entire range of orientations.

To examine spatial alignment of microvilli within a single photoreceptor we examined transmission electron microscopy (TEM) images of cross sections through individual photoreceptors. TEM images were obtained using standard EM procedures (Bozzola and Russell, 1991). Images were scanned into a computer and the orientations of microvilli in single photoreceptors were manually measured on screen using the Adobe Photoshop™ software. To minimize the potential effects of fixation and sectioning of the sample (see Nilsson et al., 1987), the orientations of 10 microvilli in each of two cells from five animals were measured (100 measurements in all). We were careful not to measure adjacent microvilli but to examine microvilli in different parts of each photoreceptor.

3. Results

In preliminary experiments, we found that a single spike or a few spikes could be obtained in response to dim or short light flashes. Spontaneous spikes irregularly occurred in nerve fibers in the dark in the absence of light stimulation. Isolated nerve fibers produced discrete responses to light stimuli polarized at different orientations. The number of spikes per stimulus of a given duration and intensity correlated in most cases with the orientation of polarization (Fig. 1A). The pattern of the response was not one of continuous firing but rather of unequal bursts throughout the light stimulus (Figs. 1A, 2A). The ratio of single receptor response at the preferred to non-preferred orientation ranged from 1.9 to 8.2 with an average of 5.3 ± 2.4 (Table 1). In three cases, nerve fibers responded to light but were insensitive to changes in polarization orientation. In seven cells, where a stable response was obtained across the full range of test intensities and polarization angles, the results matched to a \cos^2 function (with a regression correlation coefficient of $r^2 > 0.75$ for each; Fig. 1), which reflects the energy of the illumination (Sugawara et al., 1971; Labhart, 1988).

Using the spike records of the same set of cells, we calculated the number of degrees (change in polarization orientation) that would elicit a change of a single spike in the photoreceptor response (Table 1). This response changed according to the first derivative of the \cos^2 function (Fig. 1B). The least change in polarization orientation needed to elicit an additional spike occurred at 45° or 135° from the preferred/non-preferred orientation, and had values of $2.0 \pm 1.6^\circ$ per spike (range 0.3 – 4.8° ; Table 1). The least responsive orientations were in

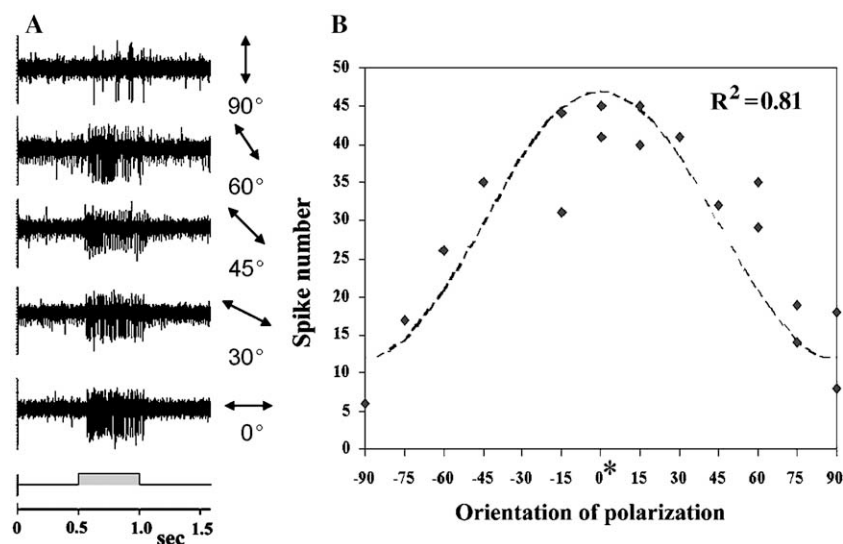


Fig. 1. (A) Spike responses of nerve fibers from the eye of a squid to a 0.5 s light stimulus (bottom trace) of equal intensity, but polarized at different orientations (illustrated by double-headed arrows). Polarization orientations in this figure were set such that the horizontal orientation produced the maximal response and the vertical polarization provided the minimal response. (B) The nerve fiber illustrated in A correlates with a \cos^2 function of the orientation of polarization (dotted line). Angles were normalized, as in A, such that the 0° produces a maximal response and 90° produces a minimal response.

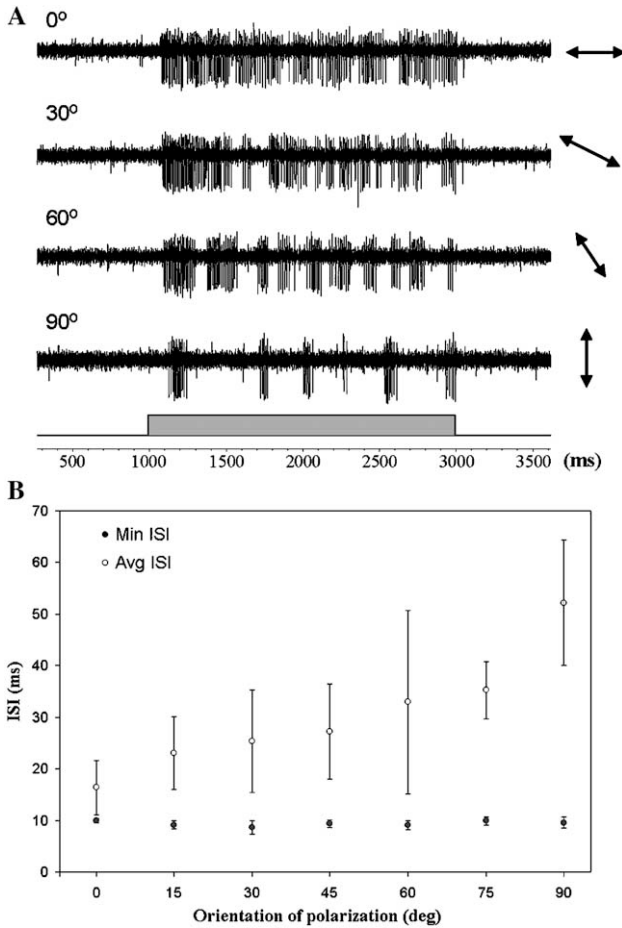


Fig. 2. (A) As the polarization orientation was changed away from the preferred angle (0°), the spike train response to a light stimulus was transformed into a series of bursts. This pattern can be seen in Fig. 1A but is clearer with this longer, 2-s light stimulus. The angles were normalized as defined in Fig. 1, where orientation of peak response is defined as 0°. Since responses were symmetrical around this preferred orientation, absolute values are presented. (B) Within the responses illustrated in A (Avg. std., $n=5$ cells), the peak inter-spike-interval (minimal ISI; closed circles) was independent of the polarization angle (Spearman rank correlation coefficient=0.060, $p=0.756$). The minimal ISI (in milliseconds) was defined as the weighted average of the peak bin in a histogram with bin width=2.5 ms and the two adjacent bins. The average ISIs (open circles, defined as the average stimulus time divided by the total number of spikes) were correlated with polarization orientation (Spearman rank correlation coefficient=0.755, $p<0.001$).

the vicinity of the preferred region and its orthogonal orientation at which changes of e-vector orientation of $9.2\pm 3.9^\circ$ were required to induce a change in the spike train (range $5.8\text{--}16.8^\circ$, $n=7$; Table 1).

In nearly all successful cell recordings, we repeated the measurements at several orientations at different time during the session. These repeat measurements allowed us to examine variations in spike response to identical stimuli from a single photoreceptor. When examining repeated measurements, recordings varied from the mean value of each setting by no more than 2.4 ± 1.7 ($n=36$) spikes.

We examined the details in the changes of a response train with changes in the orientation of polarization (Fig. 2). If the signal to the optic lobe were an average spike frequency during the stimulus, then the inter-spike-interval (ISI) should vary inversely with the total number of spikes per stimulus. We did not find that as a rule. Rather, for the most part, the minimal interval (the interspike intervals within the first burst, which were also the shortest) was unrelated to the polarization orientation (Spearman rank correlation coefficient=0.060, $p=0.756$), while the average ISI was correlated to it (Spearman rank correlation coefficient=0.755, $p<0.001$) (Fig. 2B). As the stimulus was changed so that the difference between the stimulus polarization orientation and photoreceptor's preferred orientation increased, the response spike train included more bursts. However, the ISI within a burst remained close to the minimal ISI for the entire train (Fig. 2B). As Fig. 2A illustrates, a change in number of spikes with approximately the same ISI is due to the increase in periods of silence relative to the minimal ISI. A similar phenomenon was found with changes in the overall light intensity (with or without a polarizer in the light path), i.e., the minimal ISI remained constant for a given cell. Yet, the overall number of spikes, or the average ISI, changed in correlation with the light intensity.

Variations in microvillar orientations within a single photoreceptor were small, both in individual cross-sections and for comparisons of cross-sections along the long axis of the outer segment. We found that microvilli of each cell in a particular cross-section at different depths of the outer segment were oriented to a specific orientation with an

Table 1
Potential separation of polarization orientation in photoreceptors, as measured from isolated nerve fibers

Photo-receptor	n	r^2	Spike number at preferred-orthogonal orientations (s^{-1}) (ratio)	Calculated change in e-vector orientation generating a one spike change in activity ($^\circ$)	
				Smallest (@ 45°)	Largest (@ 0°/90°)
A	26	0.83	82–10 (8.2)	0.7	9
B	19	0.81	90–12 (7.5)	2.5	10
C	13	0.77	43–6 (7.2)	0.8	7
D	7	0.75	76–40 (1.9)	4.8	17
E	16	0.87	73–24 (3.0)	0.3	6
F	12	0.86	21–5 (4.2)	3.2	11
G	13	0.79	83–13 (6.4)	1.8	8

Measurements from each cell (n , column 2) were correlated to a \cos^2 function of the orientation of polarization of the stimulating light (r^2 =regression correlation coefficient, column 3). The number of degrees correlating with a one spike change in activity was calculated using each cell's correlation function. Based on the raw data (column 4), the range of the number of degrees needed to generate this change demonstrates that the response is not equal in all angles differing from the preferred e-vector. It is smallest (average 2.0°) at 45° from the preferred/non-preferred orientations (column 5), and is largest (average 9.2°) at the preferred orientations of $0^\circ/90^\circ$ (column 6).

average standard deviation of only 1.2° (range $0.5\text{--}1.8^\circ$, $n=10$ measurements in each of 10 cells). Applying the same analysis to electron micrograph images of long sections of squid photoreceptors published by Saibil (1982, 1990a,b) and others (Zonana, 1961; Saibil and Hewat, 1987), the average standard deviation was 0.8° ($n=109$ microvilli, maximal variation between microvilli of the same cell $=5^\circ$).

4. Discussion

Two factors are of particular relevance in the biophysical limits of polarization sensitivity: the variations in microvillar alignment from mean preferred orientations between adjacent photoreceptors examining the same region of visual space; and the variations in microvillar alignment found within individual photoreceptors. The limitations from these factors that inform behavior underlie this study. Photoreceptors in a squid's retina are organized such that from the point of view of the incoming light the microvilli are mostly aligned around two predominant and orthogonal axes (Zonana, 1961; Cohen, 1973a,b; Saibil, 1982, 1990; Saibil and Hewat, 1987; Shashar et al., 2002). The microvilli within each photoreceptor are aligned tightly, presumably enabling polarization sensitivity and defining for the photoreceptor an axis of polarization to which it will be most sensitive (the receptor's "preferred e-vector orientation"). Knowing the misalignment of microvilli in a photoreceptor we can estimate the resulting reduction in polarization sensitivity. With a variation in alignment of 1.2° in the cross-section plane and 0.8° in the long longitudinal plane, we can expect a potential reduction of $\sim 7\%$ in light absorbance ($\sin [2 \times 1.2^\circ] + \sin [2 \times 0.8^\circ]$). This variation would function as an upper limit to a photoreceptor's discrimination of e-vector differences and reduce polarization sensitivity. Nonetheless, the tight alignment of the microvilli of each cell around a single orientation might explain the high polarization orientation acuity that we demonstrated electrophysiologically. Across the retina, 75% of the photoreceptors in any given region vary up to 10° from orthogonality between neighboring cells (Shashar et al., 2002). This 10° irregularity, however, could reduce the comparison of signals from neighboring photoreceptors and hence the animal's ability to detect partial polarization and impair its angular discrimination ability in polarization space.

The study of Saidel et al. (1983) related the plane of polarization to only the average spike response of a squid photoreceptor. The current study extends previous knowledge of squid visual processing by establishing some limits to discrimination of the plane of polarization. The orientation of microvilli within a photoreceptor predicts preferred and orthogonal orientations (Goldsmith, 1977). In all but three examples, we were able to identify these parameters. The magnitude of the change in spike response to a given

change in the stimulus e-vector orientation corresponded qualitatively to the magnitude of change in the first derivative of the \cos^2 function. Hence, a small sensitivity to small disparities between stimulus orientation and preferred microvillar orientation were found near the preferred/non-preferred orientation (0° or 90°); and a large sensitivity to changes in responses were recorded in ranges near 45° and 135° from the preferred orientation.

The minimal change in polarization orientation that generated a single spike change in a photoreceptor response was $\sim 2.0^\circ$. However, single spikes are unlikely to provide reliable information since the variation in spike trains for identical stimuli averaged ~ 2.4 spikes. In our case, the background average of 2.4 spikes corresponded to no less than 4.8° at the most sensitive range (and 22.1° at the least sensitive range). This result sets a lower limit to the polarization discrimination ability of a squid photoreceptor below which changes in polarization orientation are unlikely to be detected. This limit may be modified within the retina by photoreceptor connectivity to adjacent photoreceptors (Young, 1962a) and by convergence of adjacent photoreceptor axons onto cells of the "retina profunda" (Young, 1974; Saidel, 1979) where polarization antagonism may refine the analysis (Labhart, 1999). Other factors, or modes of filtration, may increase the reliability of the information and enhance the signal, which enhances the orientation discrimination ability. Shashar and Cronin (1996) reported that octopus could not detect a polarization orientation contrast of 10° . Since detecting contrast between two adjacent areas requires at least two individual photoreceptors, our results from squid (with a minimum 9.6° best separation for two cells) are consistent with these behavioral results from octopus.

Retinal inputs terminate on interneurons of the optic lobe (Young, 1962a, 1974; Saidel, 1979). Polarization-sensitive interneurons in the optic lobe may compute numerous functions with the retinal inputs; i.e., add or subtract the differences from orthogonal inputs, or accept only one orientation preference, or respond only to the existence of polarization at a given orientation without measuring its percent polarization (see Labhart, 2000). A difference signal will be maximal when the light is polarized near the preferred and orthogonal photoreceptor orientations. We refer to the difference between the outputs of a single cell to orthogonal stimuli as the polarization response ratio of the cell. In our experiments, it was found to average ~ 4.3 (0.73 dB). However, the polarization response ratio is likely to vary with light intensity (e.g., Labhart, 1988, 2000), since high light intensities may saturate a receptor cell (Lange and Hartline, 1974) or create a significant response even at the non-preferred orientation, while low intensities may be insufficient to elicit a signal even at polarization orientation near a cell's preferred orientation. A full exploration of the effects of light intensity on polarization sensitivity, as well as the measurement of sensitivity to partial polarization, requires further study.

The bursty nature of the firing suggests that visual information is not coded simply by the instantaneous spike rate. As shown in Fig. 2, when a 2-s light stimulus is varied in the orientation of polarization, the instantaneous (minimal) ISI does not change significantly although the average interval does. Similar results were obtained when varying the intensity but not the polarization of the illuminating light (or when the light was not polarized at all), suggesting that the bursty nature of the photoreceptor response is a quality of the squid visual system that partially codes light absorbance by the photoreceptor and possibly the length of the stimulus.

It remains to be determined if polarization information from individual photoreceptors is channeled separately into the retina profunda or if the responses of the two classes of photoreceptors, whose microvilli are orthogonal, converge on single central neurons, thereby producing a complex, polarization-sensitive receptive field. Such a receptive field could bring together an interaction between polarization features with other features of form. One such option could be an enhancement of borders or edges of observed objects in the relatively low-contrast aquatic environment (Balboa and Grzywacz, 2003, Chiao et al., 2005).

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