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Report

Nutritional State Modulates the Neural Processing of Visual Motion

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Summary

Food deprivation alters the processing of sensory information, increasing neural activity in the olfactory and gustatory systems in animals across phyla [1–4]. Neural signaling is metabolically costly [5–9], and a hungry animal has limited energy reserves, so we hypothesized that neural activity in other systems may be downregulated by food deprivation. We investigated this hypothesis in the motion vision pathway of the blowfly. Like other animals [10–17], flies augment their motion vision when moving: they increase the resting activity and gain of visual interneurons supporting the control of locomotion and gaze [18–21]. In the present study, walking-induced changes in visual processing depended on the nutritional state—they decreased with food deprivation and recovered after subsequent feeding. We found that changes in the motion vision pathway depended on walking speed in a manner dependent on the nutritional state. Walking also reduced response latencies in visual interneurons, an effect not altered by food deprivation. Finally, the optomotor reflex that compensates for visual wide-field motion was reduced in food-deprived flies. Thus, walking augmented motion vision, but the effect was decreased when energy reserves were low. Our results suggest that energy limitations may drive the rebalancing of neural activity with changes in the nutritional state.

Results

Hunger induces many changes in an animal's internal state, as limited resources are marshalled to increase food intake. In humans, our sense of smell may become keener, and our attention may shift from the task at hand to food [22, 23]. In food-deprived flies, the activity of peripheral olfactory and gustatory neurons is enhanced [3, 4]. Since neural signaling carries a significant metabolic cost [5–9], food deprivation may result in a decreased activity of other neurons so that limited energy reserves are adequately allocated. To investigate this possibility, we studied the motion vision pathway of food-deprived blowflies. The regulation of feeding and the neural processing of motion vision are well characterized in these highly visual animals, in which identified direction-selective visual interneurons contribute to the control of locomotion and gaze [24–26].

Flies increase the resting activity of their direction-selective interneurons during locomotion and alter their temporal frequency tuning [18–21]. These alterations may adapt the cells' dynamic signaling range to the dynamic range of visual motion the flies encounter. Similar changes in response gain and temporal frequency tuning have been found in vertebrates, including rats, mice, and zebrafish [10–15]. We reasoned that flies facing prolonged periods without food may forgo an increased investment in visual processing to conserve limited energy resources.

We recorded spiking activity from the H2 cell in flies walking on a trackball (Figure 1A). This cell supports yaw optomotor reflexes, the compensatory movements the fly performs in response to horizontal visual motion [27]. It is inhibited by the front-to-back motion that the fly experiences when walking forward and excited by the back-to-front motion mostly caused by yaw rotations. We presented the H2 cell with horizontal front-to-back motion before applying a brief test stimulus of motion in the opposite direction (Figure S1A, available online).

The Nutritional State Alters the Temporal Frequency Tuning of an Identified Direction-Selective Neuron in the Walking Blowfly

To assess the impact of reduced energy reserves on visual motion processing in walking flies, we compared the temporal frequency tuning of the responses to the test stimuli between fed and food-deprived flies (Figures 1 and 2). The H2 cell's responses are not tuned to the velocity of a grating but rather to its temporal frequency—the ratio of the angular velocity to the spatial wavelength. We defined "walking" as forward locomotion at speeds >0.5 mm/s. Walking increased both the cell's responses to temporal frequencies $\geq$ 10 Hz and the resting spike rate (Figure 1B; paired t test, Bonferroni-corrected threshold 0.0042, $p \leq 0.0039$, n = 13 flies). Walking similarly affected the activity of other cells in the same neuropil, for example, the H1 cell (Figure S1B).

When flies had been deprived of food for 3 days, walking no longer increased the cell's responses to temporal frequencies $\geq$ 10 Hz (Figure 1C; paired t test, Bonferroni-corrected threshold 0.0042, $p \geq 0.012$, n = 7 flies). Meanwhile, food deprivation in stationary trials affected neither the tuning (Figures 1B and 1C; Welch's t test, Bonferroni-corrected threshold 0.0042, $p \geq 0.04$, $n_1 = 13$ and $n_2 = 7$ flies) nor the spontaneous activity (Figure S1C; Welch's t test, $p = 0.72$, $n_1 = 13$ and $n_2 = 7$ flies).

During food deprivation for up to 3 days, the responses to temporal frequencies $\geq$ 10 Hz decreased daily (Figures 1D and 2A; Welch's t test, $p = 0.02$, $n_1 = 7$ and $n_2 = 6$ flies). When the flies were fed sucrose for 1 day after 3 days without food, the effect of walking on the processing of visual motion was restored (Figures 1D and 2A). The changes in the spontaneous spike rate showed a similar dependence on the number of days without food and increased again after 1 day of access to sucrose (Figure 2B).

These findings were unexpected, because food deprivation increases the activity of neurons of other sensory modalities in flies [3, 4]. We wondered whether 3 days without food had placed undue metabolic stress on the animals and thus compromised the activity of the cells. To gauge the metabolic stress of food deprivation, we measured the concentration of the principal sources of carbohydrate in the hemolymph—glucose and trehalose. Whereas 1 day without food significantly reduced the hemolymph level of glucose (Welch's

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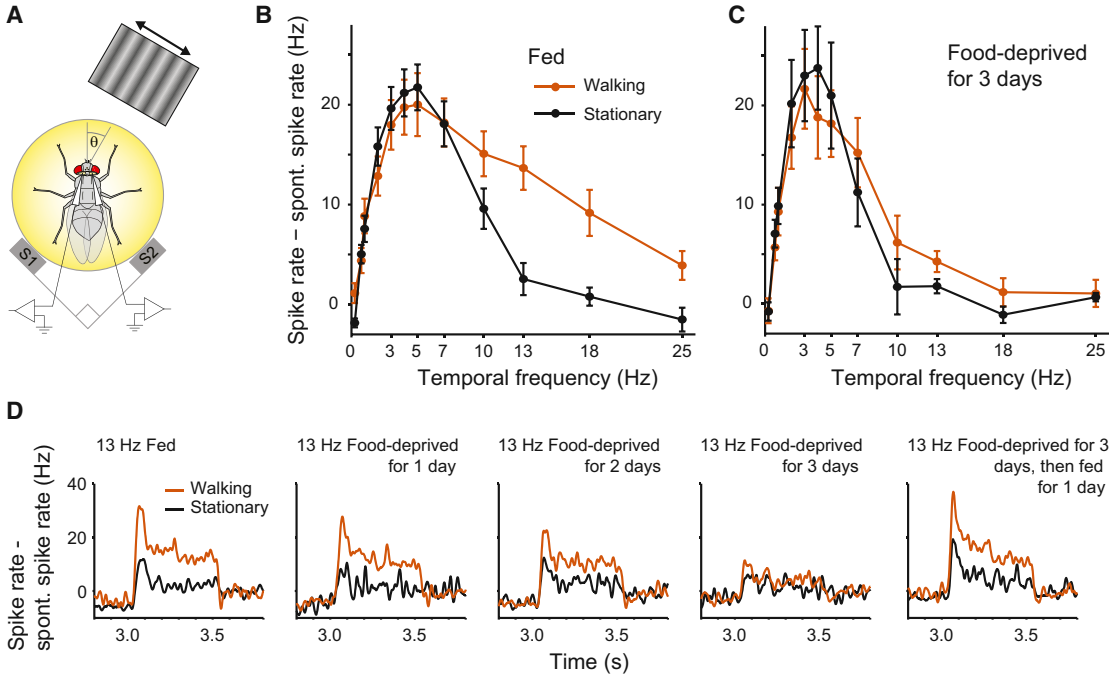

Figure 1. The Nutritional State Alters the Temporal Frequency Tuning of an Identified Direction-Selective Neuron in the Walking Blowfly

(A) Diagram of the experimental setup. The tethered fly walked on a Styrofoam ball, and two sensors (S1 and S2) tracked the ball's consequential motion. We recorded the activity of the H2 cell while visual stimuli were displayed on a monitor at an azimuth angle (θ) of 30° in the equatorial plane.

(B) Temporal frequency tuning of cells in fed flies, walking or stationary. We subtracted the spontaneous spike rate to aid comparison between the walking and stationary responses.

(C) Temporal frequency tuning of cells in flies deprived of food for 3 days. Walking no longer significantly increased the responses to fast stimuli.

(D) Mean responses to the 13 Hz stimulus. In fed flies, walking increased both the initial response and the subsequent response to the test stimuli (left panel). The effect of walking decreased with the duration of food deprivation. In flies that had been deprived of food for 3 days and were then fed sucrose for 1 day, responses to this stimulus recovered (right panel).

Error bars denote the SEM. See also Figure S1.

t test, $p < 0.001$, $n_1 = 15$ and $n_2 = 16$ flies), the mean combined concentration by mass of glucose and trehalose remained around 10 mg/ml (mean values in Figure 2C; median values and quartile ranges in Figures S2B and S2C). Thus, starvation altered the composition of hemolymph carbohydrate but did not compromise the cell's access to carbohydrate energy supplies.

Food Deprivation and the Modulation of Temporal Frequency Tuning with Walking Speed

We next studied the impact of changes in walking speed on our results. Food deprivation makes flies more active [28], and the activity of direction-selective visual interneurons increases with walking speed [19]. To access the animals' locomotor activity, we analyzed the forward walking speed

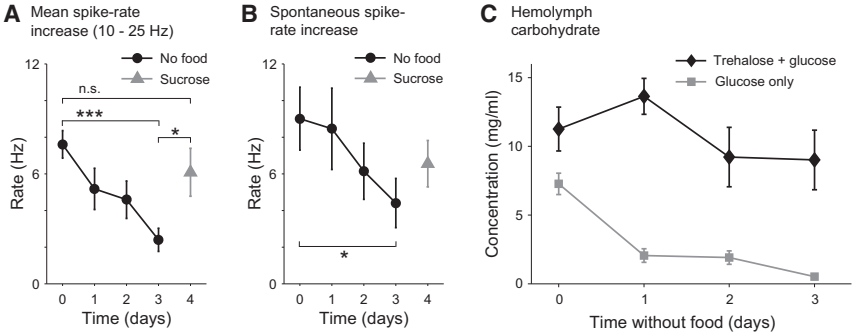

Figure 2. Food Deprivation Reduces Resting and Stimulus-Induced Activity, but Not Total Hemolymph Carbohydrate

(A) To quantify the impact of walking on the temporal frequency tuning, we calculated the mean spike-rate increase (10–25 Hz). This was the mean increase in the response to the temporal frequencies between 10 and 25 Hz (spontaneous activity was subtracted). Every day without food lowered the mean spike-rate increase ("no food"; ***Welch's t test, $p < 0.001$, $n_1 = 13$ and $n_2 = 6$ flies). After 1 day of sucrose following 3 days of food deprivation, the mean spike-rate increase was significantly elevated ("sucrose"; *Welch's t test, $p = 0.02$, $n_1 = 7$ and $n_2 = 6$ flies) and not significantly different from the value for fed flies (n.s., Welch's t test, $p = 0.32$, $n_1 = 13$ and $n_2 = 7$ flies).

(B) Walking increased the spontaneous spike rate, an effect which diminished with the duration of food deprivation ("no food"; *Welch's t test, $p = 0.049$, $n_1 = 13$ and $n_2 = 7$ flies) and partially recovered after 1 day of sucrose.

(C) Food deprivation reduced the hemolymph concentration of glucose within 1 day (***Welch's t test, $p < 0.001$, $n_1 = 15$ and $n_2 = 16$ flies) but did not significantly alter the total concentration by mass of trehalose and glucose (Welch's t test, $p > 0.08$, $n_1 = 15$, $n_2 = 16$, $n_3 = 12$, and $n_4 = 12$ flies).

Error bars denote the SEM. See also Figure S2.

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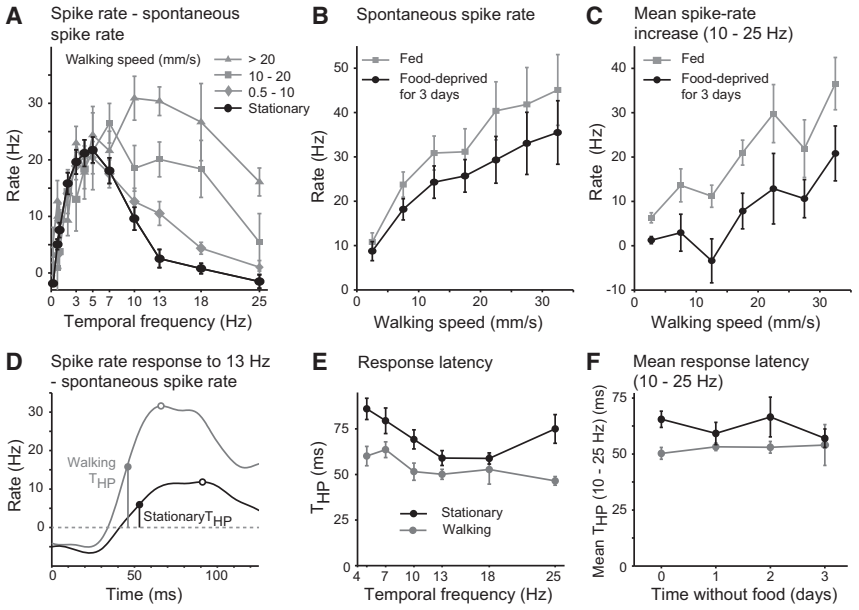

Figure 3. Food Deprivation Changes the Dependence of Spike Activity on Walking Speed, but Not the Timing of Responses

(A) Temporal frequency tuning of the cells of fed flies as a function of the walking speed. The responses to temporal frequencies between 10 and 25 Hz increased as the walking speed increased.

(B) In fed flies, the spontaneous spike rate increased with the walking speed. In flies deprived of food, the spontaneous spike rate was lower for all values of walking speed, except when flies were stationary.

(C) As in Figure 2A, we calculated the mean spike-rate increase during walking of the responses to the temporal frequencies between 10 and 25 Hz to quantify how the tuning was affected by walking. In fed flies, the mean spike-rate increase was elevated by walking speed. In flies deprived of food, the mean spike-rate increase was lower for every walking speed.

(D) Illustration of how the time to the half peak response, T_{HP}, was calculated; here, it was calculated for the mean responses to the 13 Hz stimulus. The traces can start at negative values because we subtracted the spontaneous spike rate in the period following the test stimulus. The results were qualitatively maintained when the traces were normalized to the activity at the start of the trial. T_{HP} values are indicated by filled circles (lines to the zero axis aid comparison), and open circles indicate peak responses.

(E) T_{HP} for walking and stationary trials in fed flies.

(F) Mean T_{HP} for 10–25 Hz stimuli in walking and stationary trials as a function of the number of days deprived of food.

Error bars denote the SEM. See also Figure S3.

and the yaw velocity, which describes changes in direction (Figure S3A). Consistent with previous studies, the food-deprived flies moved more quickly than fed flies (Figures S3B–S3F).

The responses to temporal frequencies $\geq$ 10 Hz became higher as the walking speed increased (Figure 3A; for 13 Hz, $p \leq 0.05$, Welch's t tests, $n_0 = 13$, $n_1 = 13$, $n_2 = 9$, and $n_3 = 8$ flies). At every walking speed, 3 days without food reduced both the spontaneous activity (Figure 3B) and the mean responses to temporal frequencies $\geq$ 10 Hz (Figure 3C). Thus, food deprivation reduced the effect of walking on the spontaneous and stimulus-induced spike rates independently of variations in walking speed. These results were qualitatively maintained when we repeated the analysis of the yaw rotation rate rather than the forward walking speed (Figures S3G–S3I): at every yaw rate, 3 days without food reduced both the spontaneous activity (Figure S3H) and the mean responses to fast temporal frequencies between 10 and 25 Hz (Figure S3I).

Walking Alters the Timing of Responses

Moving animals should respond rapidly to fast visual signals to enable effective optomotor control. While locomotion is known to affect the gain of direction-selective visual interneurons in flies, mice, and zebrafish [10–17], the impact on the neural response latency is not known. To quantify how the timing of the responses was affected by walking, we analyzed the time taken for the mean spike rate to reach half of the value of the peak response, T_{HP} (Figure 3D).

Compared to stationary fed flies, walking fed flies showed decreased T_{HP} for all stimuli (Figure 3E). In flies deprived of food for between 1 and 3 days, the mean value of T_{HP} for frequencies between 10 and 25 Hz was maintained at approximately 50 ms (Figure 3F; $p \geq 0.37$, Welch's t tests, $n_0 = 13$, $n_1 = 6$, $n_2 = 6$, and $n_3 = 7$ flies). So whereas food deprivation reduced the modulation of the resting spike rate and the temporal frequency tuning during walking, the dynamics of the responses to fast stimuli were preserved.

Reduced Optomotor Responses in Food-Deprived Flies

The H2 cell supports yaw optomotor responses, so the changes in the cell's activity should result in changes in turning responses to visual motion. To generate robust optomotor behavior, we presented wide-field visual motion to tethered flies (Figure 4A). We displayed front-to-back motion in both visual hemispheres, similar to what the fly would experience when walking forward, and followed this with a yaw optomotor test stimulus of a grating moving right to left (Figure 4A).

Three days of food deprivation reduced optomotor responses for all frequencies above 1 Hz (Figure 4B; $p \leq 0.014$, Welch's t test, n = 23 flies). The effect was particularly strong for fast stimuli: the response to the 25 Hz stimulus was lower than for the stimuli between 4 and 13 Hz in food-deprived flies ($p \leq 0.005$, paired t test, Bonferroni-corrected threshold 0.0125, n = 23 flies), which was not the case for fed flies ($p \geq 0.030$, paired t test, Bonferroni-corrected threshold 0.0125, n = 23 flies). When the food-deprived flies were allowed to recover by feeding on sucrose for 1 day, the responses increased at every temporal frequency (Figure 4B; $p \geq 0.06$, paired t test, n = 19 flies).

The mean optomotor responses increased with walking speed (Figure 4C). At walking speeds above 5 mm/s, the mean response was lower for food-deprived flies than for fed flies (Figure 4C; $p \leq 0.019$, Welch's t test, n = 23 flies). The hungry flies walked faster than the fed flies but had smaller yaw course corrections, on average, at every speed (Figure S4).

Discussion

All animals must evolve adaptive strategies to cope with a limited food supply. We have demonstrated a surprising

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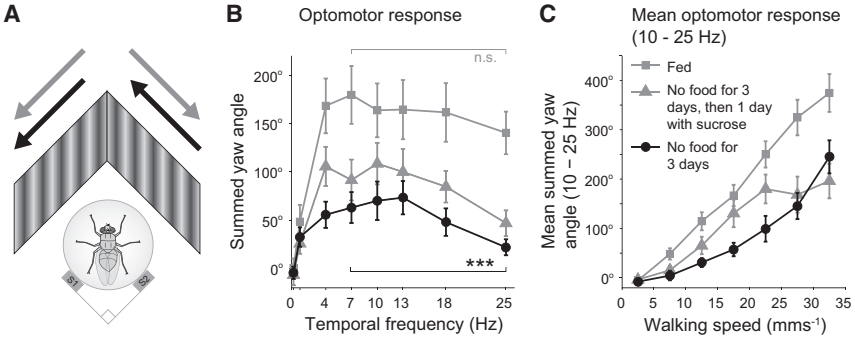

Figure 4. Food Deprivation Reduces Yaw Optomotor Responses

(A) Diagram of the experimental setup. As before, the tethered fly walked on a Styrofoam ball, and two sensors (S1 and S2) tracked the ball's consequential motion. Visual stimuli were displayed on two monitors that spanned ±105° azimuth and ±40° elevation. In each trial, a front-to-back grating was displayed on both monitors for 4 s (schematically indicated by gray arrows) before a test grating was moved at selected temporal frequencies from right to left for 4 s (indicated by black arrows).

(B) The summed yaw angle of the ball that the fly generated during the stimulus as a function of temporal frequency. Of the flies that were starved for 3 days (black circles), 19 out of 23 were given sucrose after testing and measured again the next day (gray triangles).

(C) The mean optomotor responses to stimuli at 10–25 Hz temporal frequency for binned walking speeds.

Error bars denote the SEM. See also Figure S4.

strategy in walking flies: to reduce the activity of direction-selective visual interneurons. Walking modulates the resting activity and temporal frequency tuning of the H2 cell, which requires the investment of more energy in the processing of visual information. Food deprivation reduces this activity modulation (Figures 1, 2, and 3). We have also shown that walking reduces response latency, an effect that is independent of the nutritional state (Figure 3). The H2 cell supports yaw optomotor behavior, and food deprivation reduces the optomotor responses to visual motion in general and to fast-moving stimuli in particular (Figure 4).

Previous studies have established an impact of the nutritional state on visual perception in humans [22, 23, 29] and on the activity of high-level, multisensory neurons in primates [30, 31]. Meanwhile, food deprivation has been used to motivate behavior involving visual motion [32, 33], and many studies have investigated the impact of metabolic diseases on motion vision [34–37]. However, the impact of the nutritional state on the neural basis of visual processing in healthy animals is not well understood. Our study establishes the fly as a model system for vision and feeding behavior in which we can investigate how a limited food supply alters the neural basis of visual processing.

Food deprivation is undoubtedly stressful for flies in that it affects their internal states in many ways [26, 38] and their propensity for walking [28]. We have considered some of the possible effects in our analysis. First, we verified that the energy supply was not compromised: the concentration of available carbohydrate was not significantly affected in surviving flies (Figure 2). The resting activity, responses, and latencies of stationary flies were not affected by food deprivation, further indicating that motion processing per se was not abolished. Second, differences in walking speed did not account for the effects of food deprivation: for every walking speed, the resting rates and responses to fast-moving stimuli were reduced (Figure 3). Finally, after 1 day of food following 3 days of starvation, the responses of the H2 cell to fast-moving stimuli were re-established and the resting activity was partially recovered, indicating that food deprivation did not permanently compromise the physiology of the cell. Consistent with this recovery, optomotor responses of food-deprived flies increased again after 1 day of food.

For modalities such as olfaction and gustation, changes in sensory processing help an animal to feed [3, 4, 26], for instance, by changing the preference for food with a high sucrose concentration [4]. Blowflies typically feed on stationary objects, and it is not clear how reducing the activity of motion-sensitive visual interneurons would increase feeding. Indeed, appetitive odors augment optomotor responses in the fruit fly [39]. Why, then, should the nutritional state affect motion processing? One possible explanation might be that the energy efficiency of neural processing is altered to increase the probability of survival when food is scarce. During aversive olfactory learning, food deprivation can cause fruit flies to switch from an energy-intensive form of synaptic plasticity, which involves the synthesis of new proteins, to a less robust but less energy-intensive mechanism that results in a longer lifespan [40]. We speculate that the energy efficiency of visual processing may likewise be regulated by the nutritional state to promote survival. The cost of this strategy, in the case of the H2 cell, would be a reduced performance in yaw optomotor responses, which we indeed observed in food-deprived flies (Figure 4).

Investigating the biophysical mechanisms linking the nutritional state to visual motion processing would help establish the relative importance of factors such as stress and metabolic status. Recent work has demonstrated that octopamine signaling accounts for the locomotion-induced modulation of the activity of direction-selective visual interneurons in the same neuropil containing the H2 cell [20, 21, 41–45]. Octopaminergic cells are necessary and sufficient to account for the same increases in resting activity and changes in temporal frequency tuning that food deprivation reduces [21]. Since food deprivation only affects H2 activity in walking flies and not stationary flies, one hypothesis is that it alters the activity of the octopaminergic cells in the optic lobes. Meanwhile, the observation that food deprivation does not alter the reduction in the response latency in walking flies suggests that not all mechanisms underlying walking-induced changes in visual motion processing are affected by the nutritional state.

Our results indicate that food deprivation potentially induces widespread changes in sensory processing and behavior. Food-deprived flies may not only augment their olfactory and gustatory systems to increase food intake [3, 4] but also reduce their visual processing, as we have shown. By studying the wider impact of food deprivation, we expect to better understand the principles by which limited energy resources for sensory processing are efficiently allocated under metabolic stress.

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Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures, four figures, and one table and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2014.03.005.

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