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Electron Acceptor Taxis and Blue Light Effect on Bacterial Chemotaxis

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Salmonella typhimurium and *Escherichia coli* from anaerobic cultures displayed tactic responses to gradients of nitrate, fumarate, and oxygen when the appropriate electron transport pathway was present. Such responses were named "electron acceptor taxis" because they are elicited by terminal electron acceptors. Mutant strains of *S. typhimurium* and *E. coli* were used to establish that functioning electron transport pathways to nitrate and fumarate are required for taxis to these compounds. Aerotaxis in *S. typhimurium* was blocked by 1.0 mM KCN, which inhibited oxygen uptake. Similarly, a functioning electron transport pathway was shown to be essential for the tumbling response of *S. typhimurium* and *E. coli* to intense light (290 to 530 nm). Some inhibitors and uncouplers of respiration were repellents of *S. typhimurium*. We propose that behavioral responses to light or electron acceptors involve electron transport-mediated perturbations of the proton motive force.

The chemotactic responses of bacteria are the expression of a simple sensory transduction system (20). Biochemical dissection of the system has provided new insights into the mechanisms of sensory transduction (2, 23). Attractants or repellents are detected by means of receptors. The behavioral response is proportional to receptor occupancy (26, 36) and is effected by altering the frequency of tumbling by the swimming bacteria (10, 24).

Although a great deal is now known about the chemoreceptors (2, 17, 20a) in *Salmonella typhimurium* and *Escherichia coli*, the nature of the receptor molecules and their mode of signal transmission is in need of clarification. Periplasmic proteins such as the galactose receptor (16), the ribose receptor (4), and the maltose receptor (18) have been identified, but other receptors, e.g., the serine and aspartate receptors, have been indicated through their functions rather than as physical entities. Some of the receptors appear to be part of the phosphotransferase system (3). In fact, a common feature of most of the chemotaxis receptors is that they serve a dual role as receptors for both chemotaxis and active transport. Furthermore, there is evidence that some of these receptors interact through a specific protein as the next step in the signalling process (15a, 19, 30, 33, 35, 37).

It is therefore of particular interest that intense light causes constant tumbling in *S. typhimurium* and *E. coli* (25, 38) and that this effect appears to be significantly different from the more traditional chemoeffectors in that respiration was involved in some manner. Chemotaxis to oxygen was observed by Beijerinck (8) and Engelmann (12) and further analyzed by Adler (1) and Sherris and co-workers (7, 32; for a review, see reference 9). Some clues to the mechanism of oxygen taxis were obtained in the course of studies of light effects in this laboratory (21). Moreover, it has been found in other studies that changes in the proton motive force across the membrane can be detected and responded to in the same manner as chemoeffectors (28). Accordingly, a study of light and electron transfer effects was initiated and has led to a unifying hypothesis described below.

(A preliminary account of some of the investigations in this paper has been presented [Taylor et al., Fed. Proc. **33**:1273, 1974].)

MATERIALS AND METHODS

Bacterial strains and growth conditions. Two cultures of *S. typhimurium* LT2 were obtained from B. Ames. One of the strains had become chlorate resistant-nitrate reductase deficient during repeated subculture in the Ames laboratory and is identified in this study as LT2 (Ames) (M. D. Alper, Ph.D. thesis, University of California, Berkeley, 1974). Other strains

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of *S. typhimurium* were ST1 (normal chemotaxis and motility (5) and ST171 (*cheT221 hisF8786 thyA1981*, constantly tumbling motility [6]). The strains of *E. coli* used were: W3101, obtained from J. Adler; W945*sdh* F⁻ *thr thi ara lac gal mal xyl mtl sdh tsy str* and W945*sdh frd-2* (fumarate reductase-deficient mutant obtained from W945*sdh*), from J. Guest (34); and AN120 (*uncA*), obtained from F. Gibson (11). Except where stated otherwise, cells were grown anaerobically at 30°C in Vogel-Bonner salts medium with citrate (39), fortified with the auxotrophic requirements of the strain and an additional carbon source (1%). When added, the concentration of potassium nitrate, potassium fumarate, or trimethylamine oxide in the growth medium was 30 mM.

Observation of the photoresponse. Bacteria were illuminated with a high-intensity Xenon light source as described previously (38). For normal observation the bacteria were protected from the effect of high-intensity blue light by a long-pass orange filter (Corning 3-69; 50% cut off, 530 nm) inserted in the light path between the light source and the substage condensor of the microscope (25). To observe the effect of a pulse of blue light, the filter was briefly removed, and any change in bacterial motility was observed in the microscope (×800 magnification). The microscope was fitted with either photographic (24, 36) or video recording equipment (38).

Observation of anaerobic cultures. Cultures of bacteria (optical density at 650 nm of 0.1 to 0.4) became anaerobic and could be observed when placed in a well of Lubriseal (Thomas) (22). Lubriseal was forced through a syringe onto a microscope glass slide in such a way as to form a ring approximately 1 cm in diameter. Approximately 0.1 ml of medium and cells (optical density at 650 nm of 0.1) was placed in this well, and a cover glass was then carefully placed over the well, excluding all air bubbles and marking contact with the ring of Lubriseal. The motility, growth, and light response of this microculture could then be observed over extended periods.

Observation of anaerobic taxis. Bacteria were grown to an optical density at 650 nm of 0.4 to 0.8, harvested, and suspended to an optical density at 650 nm of 0.2 to 0.4 in appropriately supplemented Vogel-Bonner medium that had been bubbled with nitrogen gas for 1 h. This culture was maintained under a stream of nitrogen for 15 to 30 min while the bacteria consumed any residual oxygen. Oxygen electrode measurements showed that such a culture would deplete all available oxygen in less than 5 min. By using a Pasteur pipette previously filled with nitrogen, the bacteria were then rapidly transferred to a slide on the microscope stage and placed under a cover glass. A continuous stream of nitrogen flowed over this slide. This procedure produced an anaerobic culture of bacteria on the slide, as shown by observations that such bacteria were immotile unless provided with a fermentable carbon source (1) and that they would not show a response to intense blue light unless provided with an electron acceptor (see Results).

Aerotaxis could be demonstrated with such a culture either by (i) turning off the nitrogen flow over the slide, after which a macroscopic band of bacteria accumulated at the edge of the cover glass, or (ii) stopping nitrogen flow and then lifting the cover glass, after which the bacteria would swim smoothly for 1 to 2 min.

Electron acceptor taxis was demonstrated by anaerobic growth of the bacteria with the appropriate electron acceptor in a sealed test tube to induce the corresponding reductase. These bacteria were then washed and resuspended in Vogel-Bonner medium plus glucose without added electron acceptor and made anaerobic under a cover glass as described above. Crystals of potassium nitrate or potassium fumarate were then added to the edge of the cover glass. A positive response to the added electron acceptor was shown by a region of smoothly swimming bacteria that appeared as the crystalline acceptor dissolved and diffused through the bacterial culture. Anaerobic chemotaxis was demonstrated in a similar fashion by adding crystals of attractants to the edge of the cover glass and noting the appearance of smoothly swimming bacteria.

RESULTS

Anaerobic motility and taxis. To study the effects of electron transfer pathways on the tactic responses of *S. typhimurium* and *E. coli*, the bacteria were incubated anaerobically in the presence or absence of a terminal electron acceptor for the respiratory chain (14). When bacteria grown on glycerol were placed in a sealed reservoir formed by a ring of Lubriseal on a microscope slide they became immotile when the oxygen was exhausted (Table 1). Glycerol was not metabolized by *S. typhimurium* in the absence of respiration, but the bacteria were not dead, because allowing air to enter the culture resulted in immediate recovery of motility. Serine and glucose are fermented and thus support motility even in the absence of oxygen or an externally added electron acceptor (1). Respiration was not required for chemotaxis to attractants such as amino acids (Table 1; reference 1). The temporal assay technique (24) revealed a smooth response to aspartate (Table 1) and serine (data not shown) in the absence as well as in the presence of electron acceptors for the electron transport system.

In contrast to the response to serine and aspartate, the tumbling response to blue light required respiration. Anaerobic *S. typhimurium* in serine or glucose medium did not show the tumbling photoresponse to blue light (Table 1). However, the response to light was restored if the anaerobic medium contained an alternate terminal electron acceptor. Fumarate, nitrate, trimethylamine oxide (18a), and oxygen were each effective in restoring the light-induced response.

Further evidence that respiration is essential

for the light response is provided in Table 2. Aerobically grown cells, glucose, and a terminal electron acceptor were added to the reservoir and sealed. Aerobic cells lack the terminal reductases required by the anaerobic electron transfer pathways, but during incubation in the reservoir, nitrate reductase, fumarate reductase, or trimethylamine oxide reductase could be induced with the appropriate electron acceptor. When an electron acceptor was present, *S. typhimurium* and *E. coli* that were induced for the appropriate terminal reductase exhibited a light response (Table 2). However, when chloramphenicol was added to the reservoir to prevent protein synthesis and induction of the terminal reductase, anaerobic *S. typhimurium* did not respond to light. The light response was restored immediately, however, upon admission of oxygen to the reservoir.

LT2 (Ames), which is deficient in nitrate reductase but has a normal fumarate reductase, did not respond to light when nitrate was the added electron acceptor but did respond to light when fumarate was present (Table 2). Conversely, *E. coli* W945*sdh frd-2*, which lacks fumarate reductase but has normal nitrate reductase, tumbled in blue light if nitrate was present but not when fumarate was the acceptor. Thus, the terminal portion of an electron transfer pathway must be functional before the light response is observed.

Aerotaxis and electron acceptor taxis. Aerotaxis was measured by a temporal assay in which an anaerobic culture of bacteria was transferred to a microscope slide under a stream of nitrogen gas. When the anaerobic bacteria were

TABLE 1. *Effect of electron transport on chemotaxis and photoresponse in S. typhimurium LT2*[a]

Additions to medium[b]	Anaerobic motility pattern		Motility pattern in blue light	
	In absence of gradient	After temporal aspartate gradient	Anaerobic	Aerobic
Glycerol	Immotile	Immotile	Immotile	Constant tumbling
Glycerol and KNO_3	Random[c]	Smooth	Constant tumbling	Constant tumbling
Serine	Random	Smooth	Random	Constant tumbling
Serine and KNO_3	Random		Constant tumbling	Constant tumbling
Glucose	Random	Smooth	Random	Constant tumbling
Glucose and KNO_3	Random		Constant tumbling	Constant tumbling
Glucose and fumarate	Random		Constant tumbling	Constant tumbling
Glucose and trimethylamine oxide	Random		Constant tumbling	Constant tumbling

[a] The bacteria were grown aerobically and then transferred to an anaerobic chamber where chemotaxis or the response to blue light was observed as described in the text. The motility patterns noted were those observed 5 s after addition of attractants or exposure of the bacteria to blue light in the indicated medium.

[b] Vogel and Bonner medium without citrate (see the text). Concentration of carbon source, 1%; electron acceptor, 30 mM.

[c] Random behavior consists of alternating periods of smooth swimming and tumbling and occurs in the absence of a detectable stimulus.

TABLE 2. *Motility of anaerobic S. typhimurium in blue light in the presence and absence of terminal electron acceptors*[a]

Strain	Additions to medium		
	Glucose	Glucose + KNO_3	Glucose + fumarate
S. typhimurium			
LT2 (wild type)	Random	Constant tumbling	Constant tumbling
LT2 + chloramphenicol[b]	Random	Random	Random
LT2 (Ames) (nitrate reductase$^-$)	Random	Random	Constant tumbling
E. coli			
W945*sdh* (fumarate reductase$^+$)	Random	Constant tumbling	Constant tumbling
W945*sdh frd-2* (fumarate reductase$^-$)	Random	Constant tumbling	Random

[a] Experimental procedure is described in Table 1. The motility patterns were observed 5 s after the bacteria were exposed to intense blue light in the indicated medium.

[b] Chloramphenicol (100 μg/ml) was added before the addition of nitrate or fumarate.

exposed to air they immediately suppressed tumbling and swam smoothly for 1 to 2 min. The aerotactic response is illustrated in Fig. 1 using *S. typhimurium* ST171, a mutant with constantly tumbling motility. The smooth-swimming response to a temporal gradient of oxygen is analogous to the smooth-swimming response to a temporal gradient of attractant (24) and is a more convenient assay for aerotaxis than the methods previously used (7, 12). The smooth aerotactic response was blocked by KCN (Fig. 1C) at concentrations (1 mM) that inhibited oxygen uptake by *S. typhimurium* as measured with an oxygen meter. Azide inhibited oxygen uptake in ST1 by 80 to 90% but did not prevent the aerotactic response.

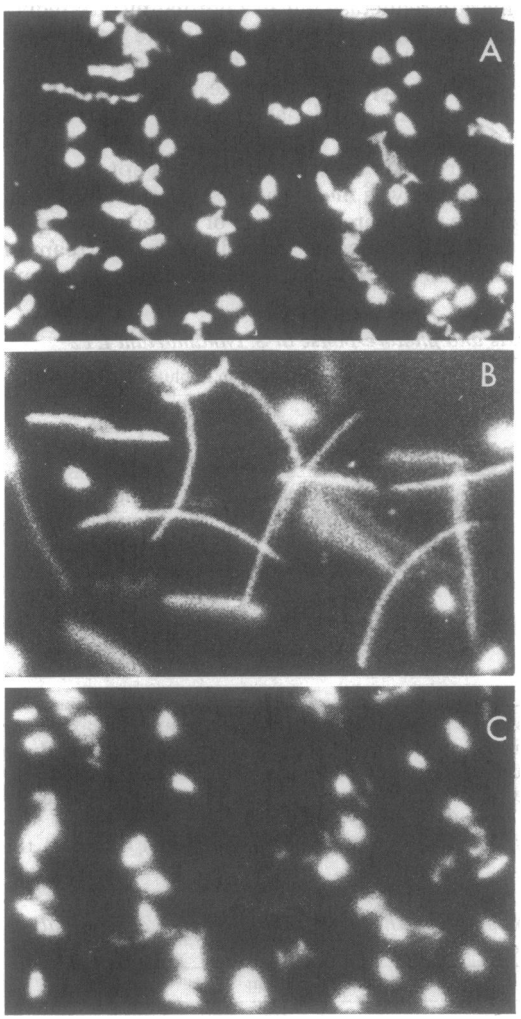

FIG. 1. *Response of S. typhimurium ST171 to a temporal gradient of oxygen. (A) Constantly tumbling motility of the anaerobic bacteria in Vogel-Bonner-citrate medium with added glucose before exposure to oxygen. See the text for details of the procedure. Immotile bacteria appear as rods; constantly tumbling bacteria appear as blurs. The photograph was exposed for 1 s. (B) Smooth motility of ST171 5 s after exposure to air. White tracks are smoothly swimming bacteria. (C) Behavior of ST171 after exposure to oxygen, but with KCN (1.0 mM) added to the medium before exposure to oxygen. No smooth swimming resulted. The photograph was made 5 s after the bacteria were exposed to oxygen.*

Taxis to nitrate and fumarate was examined using a modification of the method used to observe aerotaxis. The anaerobic cells on the microscope stage were maintained under a stream of nitrogen, and solid KNO_3 or potassium fumarate was added to the edge of the culture. A smooth-swimming response that spread throughout the medium was indicative of taxis to the acceptor tested. The responses of *S. typhimurium* ST171 to nitrate and fumarate are shown in Fig. 2. Electron acceptor taxis, as we have named the response, requires prior induction of the pathway for electron transfer to the acceptor. Nitrate reductase deficiency [*S. typhimurium* LT2 (Ames)] prevented taxis to nitrate but not to fumarate (Table 3). Similarly, a defect in fumarate reductase (*E. coli* W945*sdh frd-2*) prevented fumarate taxis but not nitrate taxis.

Response of the bacteria to uncouplers and inhibitors of oxidative phosphorylation. The effects of some uncouplers and inhibitors of oxidative phosphorylation on the behavior of the bacteria were determined. Aerobic, wild-type *S. typhimurium* (ST1) in Vogel-Bonner–citrate medium showed a brief (less than 30 s) period of constant tumbling when rapidly exposed to 5 mM NaN_3, 1 mM KCN, or 10^{-7} M carbonylcyanide *m*-chlorophenylhydrazone. 2,4-Dinitrophenol did not affect the behavior of the bacteria at low concentrations, although both 10 mM dinitrophenol and 10^{-5} M carbonylcyanide *m*-chlorophenylhydrazone caused loss of motility. Thus, for *S. typhimurium* as for *Bacillus subtilis* (31), some respiratory inhibitors and uncouplers of oxidative phosphorylation act as repellents at low concentrations. Another uncoupler (dinitrophenol) had no effect on swimming of *S. typhimurium* until the concentration was increased to levels at which motility was abolished.

In *E. coli* AN120 (*uncA*; 11), oxidative phosphorylation is inhibited by a mutation in the energy-transducing ATPase. To determine whether oxidative phosphorylation is required for aerotaxis, the response of AN120 to oxygen was investigated and found to be normal. The response of AN120 to blue light was also normal. Evidently ATP is not the signal that regulates the behavioral response to oxygen or blue light.

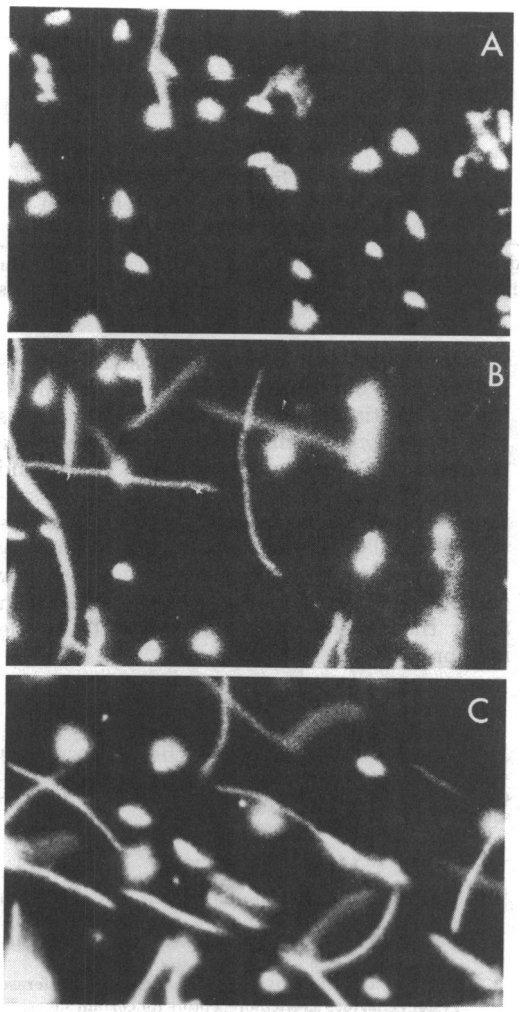

FIG. 2. *Response of S. typhimurium ST171 to a gradient of electron acceptor. ST171 were grown anaerobically in the presence of electron acceptor and then washed and suspended in Vogel-Bonner-citrate medium with added glucose but without electron acceptor. (A) Motility of anaerobic ST171 in the medium before addition of electron acceptor. (B) Smooth motility after addition of KNO_3 crystals. (C) Smooth motility after the addition of potassium fumarate crystals. Exposures were made 5 s after the addition of electron acceptor.*

DISCUSSION

The results demonstrate that a functioning electron transport chain is required for response to terminal electron acceptors and to intense blue light. The electron transport pathways must be those appropriate for the terminal electron acceptor present in the medium. For instance, the response to blue light in a nitrate-supplemented medium, as well as taxis towards nitrate, requires the presence of an electron transfer pathway involving nitrate reductase. The same is true for fumarate. The response to oxygen appears to be dependent on the terminal oxidase, cytochrome *o*, and is inhibited by cyanide at concentrations that inhibit cytochrome *o*. We have concluded that the receptor for electron acceptor taxis is the terminal component of the appropriate electron transport pathway. That is, the receptors for taxis to oxygen, nitrate, and fumarate are cytochrome *o*, nitrate reductase, and fumarate reductase, respectively. Miller and Diehn (29) have proposed that cytochrome oxidase is also the receptor for aerotaxis in *Euglena gracilis*.

Perturbation of the electron transport system is sufficient to alter the swimming behavior, but the mechanism by which the signal is transmitted remains to be explained. ATP has been excluded as the regulator of the behavioral response because the *uncA* mutant AN120 showed a normal response to oxygen and blue light. A second alternative is that the proton motive force is the agent affecting the behavior. It has previously been shown for *B. subtilis* that changes in the membrane proton motive force cause behavior changes similar to those of chemoeffectors (28, 31). A decrease in the proton motive force causes transient tumbling, and an increase causes transient smooth swimming. The present studies are consistent with a similar influence of the proton motive force on the motility of *S. typhimurium* and *E. coli*.

The exposure of anaerobic bacteria to terminal electron acceptors increases the flow of electrons and the proton motive force. In *E. coli*, an increase in the proton motive force has been measured after addition of oxygen (13) or fumarate (27) to an anaerobic culture. The change in proton motive force seen in those experiments should be sufficient to cause the smooth-swimming response observed here. Likewise, Goral and Taylor (W. W. Goral and B. L. Taylor, Clin. Res. 27:5A, 1979) observed that the smooth-swimming response to oxygen by *Bacillus cereus* is associated with membrane repolarization. Ongoing studies of aerotaxis in *S. typhimurium* have revealed a similar relationship between proton motive force and aerotaxis in that organism (D. J. Laszlo and B. L. Taylor, unpublished data).

The effect of uncouplers and the blue light effect are also consistent with this hypothesis. The tumbling response to blue light could be explained by photooxidation of a specific flavoprotein photoreceptor (25, 38), which would inhibit the flow of electrons in the respiratory chain and thus decrease the proton motive force. As a result, light which decreased the proton

TABLE 3. *Motility pattern of anaerobic S. typhimurium in temporal gradients of various electron acceptors*[a]

Strain	Addition to growth medium	Motility pattern with electron acceptor		
		Oxygen	Nitrate	Fumarate
LT2 (wild type)	None	Smooth	Random	Random
	Nitrate	Smooth	Smooth	Random
	Fumarate	Smooth	Random	Smooth
LT2 (Ames) (nitrate reductase$^-$)	Nitrate	Smooth	Random	Random
	Fumarate	Smooth	Random	Smooth

[a] Bacteria were grown anaerobically in the indicated medium, washed three times, and resuspended for anaerobic observation in the same medium as described in the text. The motility pattern was then noted 5 s after addition of the indicated electron acceptor.

motive force would cause tumbling. Phototaxis in the photosynthetic *Rhodospirillum rubrum* is mediated by changes in membrane potential (15).

The postulated role of the proton motive force in the blue light response of *S. typhimurium* suggests a mechanism for the previously unexplained smooth swimming and paralysis caused by blue light (38). When *S. typhimurium* were continuously illuminated by intense blue light, the bacteria initially tumbled constantly, but after 5 to 8 s their motility became smooth (38). If illumination was continued for about 30 s, the bacteria became paralyzed. Recent experiments (D. J. Laszlo, W. W. Goral, and B. L. Taylor, manuscript in preparation) have revealed a threshold proton motive force in *S. typhimurium* that is required for tumbling. This threshold for tumbling is higher than the threshold for motility, so that there is a range of proton motive force within which the bacteria are always smooth swimming. The tumbling threshold has also been observed by Khan and Macnab (personal communication). These results suggest that the tumbling, smooth swimming, and paralysis following exposure to blue light may all result from a decrease in the proton motive force. We propose that continuous illumination interrupts electron transport and that the proton motive force continues to fall steadily. Constant tumbling is the initial response to falling energy levels, but after the proton motive force falls below the tumbling threshold the bacteria become smooth swimming. Eventually membrane energy falls below the motility threshold, and the bacteria become paralyzed. The observed velocities of *S. typhimurium* are consistent with this hypothesis. In light-induced smooth swimming, as in anaerobic smooth swimming, the bacteria are noticeably slower than aerobic bacteria that are swimming smoothly in response to serine. Slower velocities are to be expected where membrane energy levels are decreased.

The use of membrane potential as a signal to the behavioral system is one pathway but not the exclusive avenue for behavioral changes. In *B. subtilis* the response to chemoattractants is independent of any significant change in membrane potential (28). It is likely that the same is true for *S. typhimurium*. A drop in membrane potential can signal suboptimal conditions, and an increase can indicate more favorable surroundings. Hence any perturbation which alters the potential would elicit a response. In this way the bacteria could optimize their energy supply without requiring separate receptors for each agent that affects the energized state of the membrane.

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