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FERROMAGNETIC MATERIAL IN THE EASTERN RED-SPOTTED NEWT, *NOTOPHTHALMUS VIRIDESCENS*

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Summary

Behavioral results obtained from the Eastern red-spotted newt (*Notophthalmus viridescens*) led to the suggestion of a hybrid homing system involving inputs from both a light-dependent and a non-light-dependent mechansim. To evaluate the possible role of a receptor based on biogenic magnetite in this animal, we performed magnetometry experiments on a set of newts previously used in behavioral assays. The natural remanent magnetization (NRM) carried by these newts was strong enough to be measured easily using a direct-current-biased superconducting quantum interference device functioning as a moment magnetometer. Isothermal remanent magnetizations were two orders of magnitude higher than the NRM, suggesting that ferromagnetic material consistent with magnetite is present in the body of the newt. The NRM has no preferential orientation among the animals when analyzed relative to their body axis, and the demagnetization data show that overall the magnetic material grains are not aligned parallel to each other within each newt. Although the precise localization of the particles was not possible, the data indicate that magnetite is not clustered in a limited area. A quantity of single-domain (SD) magnetic material is present which would be adequate for use in either a magnetic intensity or direction receptor. Our data, when combined with the functional properties of homing, suggest a link between this behavioral response and the presence of ferromagnetic material, raising the possibility that magnetite be involved at least in the map component of homing of the Eastern red-spotted newt.

Key words: eastern red-spotted newt, *Notophthalmus viridescens*, magnetite, orientation, homing.

Introduction

The Eastern red-spotted newt is a terrestrial vertebrate known to exhibit two forms of orientation behavior based on the Earth’s magnetic field. One is a simple compass orientation (Phillips, 1986a), in which a fixed (shoreward) trained directional heading relative to the magnetic field is maintained. The other is a magnetic effect on navigation or homing (Phillips, 1987), which requires both some form of ‘map’ information to determine the correct geographic position relative to home and a compass to orient in the homeward direction. In a subsequent study (Phillips et al., 1995), newts were found to use true navigation, *i.e.* to return to the origin of a displacement (‘home’) without access to familiar landmarks or goal-emanating cues, and without knowledge of the displacement route.

The compass component of homing could be derived from the same pathway (or mechanism) as the one involved in the simple compass orientation. Nevertheless, subsequent results strengthened the hypothesis that the newts were using separate magnetoreception systems in these two forms of orientation. When a simple compass is needed, newts appear to use an axially sensitive receptor system (i.e. one which responds only to the magnetic field inclination), whereas their homing response exhibits a polar sensitivity (i.e., sensitivity to the horizontal polarity of the magnetic field; Phillips, 1986b). Subsequent studies indicate that shoreward and homeward magnetic compass orientation are affected by the wavelength of light (short-wavelength and full visible spectrum vs. long-wavelength) in different ways (Phillips and Borland, 1992, 1994).

On the basis of their findings, Phillips and Borland (1992, 1994) suggested that a light-dependent magnetic compass was used for the shoreward orientation response, whereas the homing response was mediated by a “hybrid mechanism”. This latter response was proposed to combine information from the light-dependent compass and a non-light-dependent system. However, the debate continues as to whether the light effect is a primary feature at the level of the biophysical magnetic compass transducer, or an influence of light on the animal’s subsequent behavior (Kirschvink et al., 1997). There is agreement that the sensitivity needed for magnetic navigation is incompatible with a response produced by an optically-driven radical pair recombination system (Schulten, 1982), whereas it is within the theoretical range for a magnetite-based system (Kirschvink and Walker, 1985).

In the 35 years since Lowenstam (1962) proposed the hypothesis that ferromagnetic material could serve as a possible magnetic transducer, biogenic magnetite particles have been found in a wide variety of organisms (e.g. Gould et al., 1978; Kirschvink et al., 1985; Walcott et al., 1979; Wiltschko and Wiltschko, 1995), some of which have provided behavioral and neurophysiological evidence of Earth-strength magnetic field sensitivity (e.g. Beason, 1989, 1992; Beason and Semm, 1987; Semm and Beason, 1990; Walker et al., 1997). In parallel with these discoveries, numerous biophysical models have been developed indicating how small magnetite crystals might be transduced into neurological signals that could be used by an animal (Kirschvink et al., 1993; Kirschvink and Gould, 1981; Kirschvink et al., 1992a; Kirschvink and Walker, 1985; Yorke, 1979). Given the properties of the newt's homing response, Phillips and Borland (1994) assumed that the non-light-dependent part of the "hybrid mechanism" could be magnetite-based.

To assess this suggestion, the present experiments took advantage of the magnetometry facility at the California Institute of Technology. A group of newts that had been tested for homing ability by the Phillips group at Indiana University was used to test for any presence of ferromagnetic material. Our data show that the red-spotted newt contains magnetic particles with properties that are consistent with magnetite.

Materials and methods

Magnetic measurements were carried out on a group of 18 adult male newts *Notophthalmus viridescens* previously subjected to magnetic orientation experiments (the results of which will be presented elsewhere: J. B. Phillips and S.C. borland, in preparation). These animals were collected in ponds to the southwest and southeast of Bloomington, Indiana, USA. They were anesthetized with MS-222 at least 24 hours after testing at Indiana University, frozen in liquid nitrogen, and then shipped on dry ice to Caltech for magnetic measurements. The newts were kept frozen because they contain relatively high levels of the toxin tetrodotoxin in their skin (Brodie et al., 1974); indeed a preliminary attempt to measure any magnetization carried by some newts of the same species suggested that this toxin might be released into the body after death and could interfere with any magnetization carrier present in the body; soaking them in liquid nitrogen would prevent this by suddenly blocking all the physiological processes). The experiments used ultrasensitive moment magnetometers (2G Enterprises®) employing direct current-biased superconducting quantum interference devices (SQUIDs). These devices are designed to measure the total ferromagnetic moment of samples placed within a Helmholtz-coil pickup loop (Fuller et al., 1985). In order to assess the characteristics of any ferromagnetic material they might contain, the frozen newts were subjected individually to several rock magnetic experiments: the natural remanent magnetization (NRM) vector was initially measured and demagnetized progressively using alternating magnetic fields (Af demagnetization). The newts were then given an anhysteretic remanent magnetization (ARM) in progressively stronger biasing fields, the strongest of which was then Af-demagnetized. Next, they were given an isothermal remanent magnetization (IRM) in a peak pulse field of 100mT, which was then Af demagnetized. Finally, a complete IRM acquisition spectrum was conducted in log-spaced steps up to 1 Tesla. During the measurements the newts were kept frozen by a flow of dry, cold-filtered air inside the magnetometer. The temperature was never allowed to rise above -40° C (223 K) to –50° C (233 K). All measurements were performed in magnetically shielded environments, dust-free in the case of IRM and ARM experiments. The newts were suspended on a thin nylon monofilament line, moved by a stepping motor between the loading and measurement regions of the magnetometer, and subsequently the magnetization and demagnetization coils. As we cannot control the temperature precisely inside the magnetometer, we tentatively performed a rough "warming experiment" on two newts to assess the presence or absence of very fine, superparamagnetic (SPM) grains. Each sample was soaked in liquid nitrogen (-196° C; 77 K), then given an IRM with a 1T pulse. Following this, the sample remanence was monitored every few seconds for at least the following 11 min as the sample was warming in an atmosphere with a temperature between -18° and 0° C (255 and 273 K). This procedure was then repeated once without the 1T pulse and finally a second time with this pulse.

Results

A natural magnetic remanence was detected in all the newts examined, as indicated in Table 1. The NRM ranges from 0.58×10^{-11} to 25.4×10^{-11} Am^2, with an average of 4.40×10^{-11} Am^2, whereas the background noise levels were approximately 1.1×10^{-12} Am^2 (mean ± S.D., N=18). The NRM directional analysis relative to the anterior of the head shows no particular direction of alignment among the newts (p>0.30, test of uniformity applied to the distribution of the 18 NRM directions; Fisher et al., 1987). Experiments utilizing the alternating-field demagnetization of the NRM were designed to detect weather different subsets of magnetic particles within each newt were aligned in particular directions; these give a qualitative indication of the net directions carried in each newt by grains in different coercivity ranges (Fig. 1). This distribution is also statistically random using a positive test of uniformity (Fisher et al., 1987), except for three newts. For these latter, however, though the previous statistical test gives a probability of uniform distribution lower than 5%, the scatter in the grain distribution is high (see, for example, newt X in Fig. 1). Thus, in each newt the magnetic grain magnetizations are not more or less aligned along a specific direction relative to the body of the newt, instead their directions are scattered rather randomly. However, the methods used in these experiments did not make it possible to determine whether the net direction of grains within a particular coercivity range was the same in different individuals.

Table 1. *Intensity and direction of the Natural Remanent Magnetization measured in individual* Notophthalmus viridescens

Newt	NRM x 10^{-11} (A.m^2)	D (degrees)	I (degrees)	α95	*k*
A	1.47 ± 0.05	347.9	32.0	1.1	1166.6
C	25.44 ± 0.10	136.5	-35.7	0.9	1946.1
E	5.92 ± 0.03	284.4	23.8	0.8	2763.8
F	1.94 ± 0.06	305.5	26.2	1.3	976.7
G	6.26 ± 0.08	146.8	-1.5	0.5	8438.3
H	7.25 ± 0.04	47.3	28.2	0.9	2309.2
J	2.79 ± 0.12	298.5	-18.6	2.2	982.6
L	1.88 ± 0.03	357.9	5.6	1.6	671.5
M	1.65 ± 0.02	92.6	-1.3	1.6	564.0
N	1.94 ± 0.01	128.3	-2.3	1.3	1296.5
O	0.58 ± 0.03	291.3	-11.5	2.2	244.7
P	1.37 ± 0.01	97.2	-11.3	1.7	410.3
Q	8.89 ± 0.03	40.6	39.5	0.7	3978.5
T	1.02 ± 0.03	14.9	-9.6	1.1	1579.5
W	1.05 ± 0.03	4.3	-39.1	1.9	343.1
X	4.76 ± 0.08	133.8	66.6	1.0	1506.0
Y	1.30 ± 0.03	247.3	14.6	2.0	437.3
Z	3.66 ± 0.06	105.0	53.3	2.0	471.1

NRM, intensity of the natural remanent magnetization; values are means ± S.D. (n=18).

D, I, the declination (azimuthal angle between the horizontal component of the NRM and the anterior head of the newt, ranging from 0° to 360°, positive clockwise) and inclination (vertical angle between the horizontal and the NRM, ranging from -90° to +90° and defined as positive downward) of the NRM, respectively.

α95 and k, 95% confidence cone and the precision parameter of the Fisher's (1953) statistics, respectively.

The NRM shows no preferred direction of orientation among the newts (n=18, p>0.30; probability of uniform distribution; Fisher et al., 1987; non significant preferred orientation= p>0.05).

The characteristics of the magnetometer did not allow even a rough estimate of the localization of grains in the body of the newt. However, the magnetic signal recorded along the body (obtained by measuring the magnetization for different longitudinal distances between the nose of the newt and the magnetometer sensors; data not shown) has a very consistent pattern among the newts and is definitely not compatible with the idea that the magnetic particles are clustered in a unique area (at least less than 0.5-1 mm long). Indeed, the magnetization carriers seem to be spread out in a large volume of the body of the newt. However, the anatomy of their distribution and the volume they occupy are both unknown. It was not possible for example, to determine whether particles within a particular coercivity range were more localized in distribution, as might be the case if only a subset of particles contributing to the NRM were located in a specialized sensory structure.

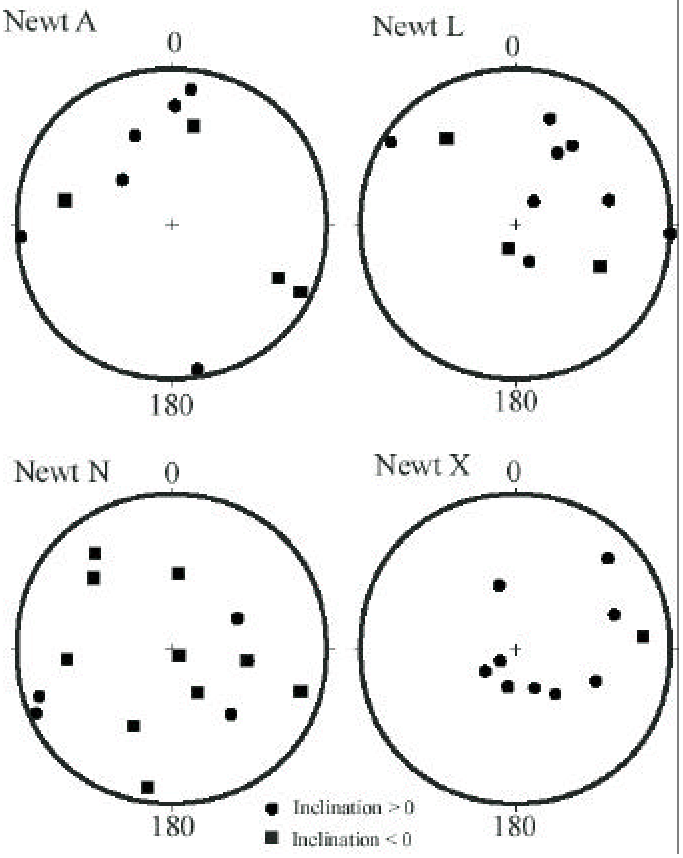

Figure 1. Equal-area projection of mean magnetic grain directions deduced from the alternating-field (Af) demagnetization of the natural remanent magnetization (NRM). The Af demagnetization of the NRM was performed in order to have an idea of whether the grain magnetizations were all aligned along a preferential direction or not. The additive property of magnetization (a vector) is combined with the Af demagnetization to separate any non-aligned component of the magnetization. The graphic procedure used here is to view the magnetization vector directions as radiating from the center of a unit sphere and to display the intersection of these vectors with the sphere. The sphere and the points of intersection of the vectors with it are then projected onto the horizontal plane. Black solid squares are for negative inclinations and grey solid circles for positive inclinations, i.e. upward and downward relative to the horizontal plane, respectively. The declination is measured around the perimeter of the projection, clockwise from 0° (0° and 180° are oriented toward the nose and the tail of the newt, respectively). The inclination is measured from 0° at the perimeter of the projection to ±90° at the center of the projection. Each point represents the mean direction for grains with coercivity comprised between two successive steps of demagnetization. The results indicate that grain magnetizations are not aligned along a preferential direction relative to the body of the newt.

There is a consistency in the characteristics of acquisition and Af demagnetization for IRM and ARM among the newts:

Fig. 2 displays the mean patterns with their standard deviation. The fact that the newts gain and lose magnetization in such experiments yields evidence for the presence of ferromagnetic materials in the newt's body. The magnetic characteristics given by IRM acquisition and Af demagnetization are displayed in Table 2. The saturated IRM values are two orders of magnitude higher than the NRM, with a mean of 2.08 ± 1.13 nAm^2, with saturation arising between applied fields of 400 and 600 mT, but mainly around 400 mT. The ARM acquisition (Fig. 2b) shows the same pattern as for the chiton teeth (Cisowski, 1981) which contains biogenic magnetite (Kirschvink and Lowenstam, 1979). All these results are consistent with SD-grained magnetite with a high intergrain interaction (Cisowski, 1981) and suggest that the ferromagnetic crystals are disposed in interacting clumps. On the other hand, the decrease in magnetization exhibited in our "warming experiment" (Fig. 3) suggests that the newts also contain SPM grains, as do other organisms (Kirschvink and Gould, 1981; Kirschvink and Woodford, 1991).

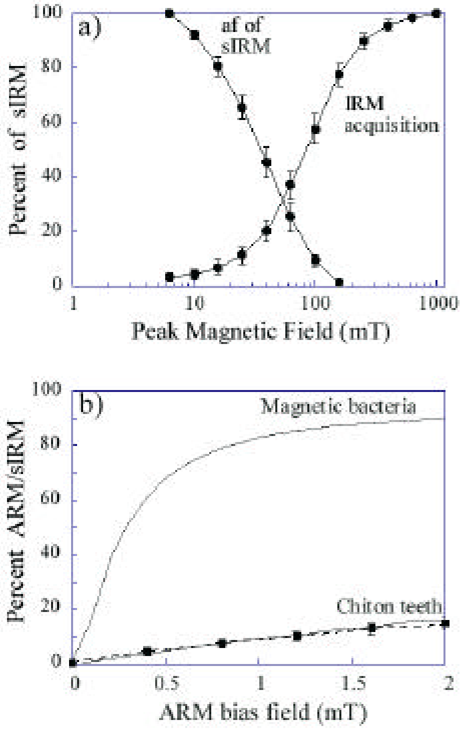

Fig 2. Mean pattern of magnetic behavior of the newt's magnetization carriers. a) The curve labeled "IRM acquisition" shows the relative magnetic moment remaining after a brief exposure to a magnetic pulse of the indicated strength. The tendency of the curve to flatten at high field levels is characteristic of the magnetite-maghemite solid solution series; most other ferromagnetic minerals saturate in fields higher than 1T. The curve labeled "af of sIRM" shows the progressive alternating-field demagnetization of the saturation IRM. The magnetic field value at which these two curves cross is a good estimate of the remanent coercive force (Hrc). The ordinate of the intersection point for non-interacting particles occurs at the 50% value; a depression or shift in this position is an indication of particle clumping effects. b) The acquisition of ARM. The upper control curve shows data from a sample of magnetotactic bacteria in which the magnetite crystals are aligned in linear chains and have few other interparticle interactions, whereas the lower control curve is from a sample of magnetite from chiton teeth, which are SD crystals but are highly interacting. The solid squares bound by a dashed line represent the mean pattern for the newt ferromagnetic material. This pattern suggests the ferromagnetic grains are in small interacting clumps.

Table 2. *Magnetic characteristics as deduced from the isothermal remanent magnetization acquisition and alternating-field demagnetization experiment.*

Newt	sat. field (mT)	mdf (mT)	Hrc (mT)	sIRM (nA.m^2)
A	400	32.2	51.3	2.87
C	400	32.2	48.7	4.57
E	400	41.0	59.9	1.41
F	400	38.9	56.9	1.38
G	520	37.6	55.0	2.04
H	400	36.9	52.2	4.26
J	600	32.2	52.2	3.71
L	400	29.0	43.2	2.83
M	400	33.3	52.2	1.55
N	460	33.9	52.2	1.10
O	460	47.0	71.2	1.85
P	400	36.3	53.1	1.90
Q	400	30.0	46.2	0.75
T	400	39.6	59.0	0.76
W	400	38.9	61.0	1.65
X	400	37.0	59.9	1.11
Y	400	34.5	52.2	1.68
Z	400	39.6	58.9	2.04

Sat. field, saturating magnetic field (field required to produce the IRM saturation); mdf, median destructive field (field that removes half of the saturated IRM); Hrc, remanent coercive force (field deduced by the intersection of the IRM acquisition curve and af demagnetization curve) ; sIRM, saturated IRM.

The saturating magnetic field for isolated SD magnetite grains is usually =300 mT, however it may extend beyond this value for strongly interacting SD magnetite grains (Cisowski, 1981). Moreover, for non-interacting SD grains, Hrc should be identical to the mdf (Wohlfarth, 1958).

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Discussion

This study indicates the presence of ferromagnetic material in the newt body. The consistency of the magnetic properties among the newts makes it unlikely that the observed magnetizations could be the consequence of occasional external contamination. Although it was impossible to define the spatial disposition of the magnetic particles, our results suggest they form clumps that could be situated in rather different areas of the body. This would not be unusual given that some animals, and even humans, have been shown to contain ferromagnetic particles in a variety of different tissues (e.g. Grassi-Schultheiss et al., 1997; Kirschvink et al., 1992b; Kirschvink and Walker, 1986; Wiltschko and Wiltschko, 1995). This suggests that a significant proportion of the particles may not be involved in magnetoreception, but instead may have a non-sensory function. However, at the moment, this non-sensory function remains unknown.

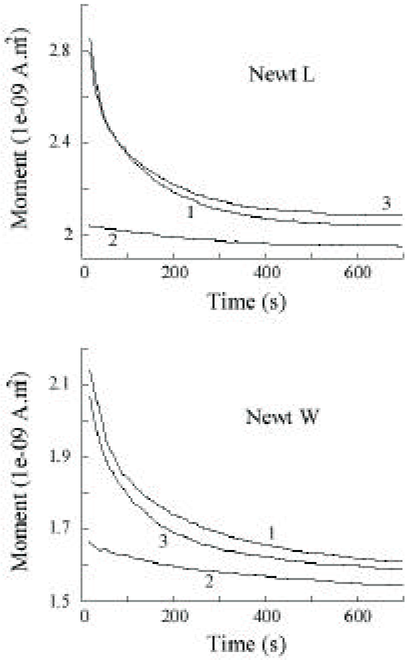

Figure 3. Variation of the remanence acquired at low temperature monitored during zero-field heating. Néel (1949) has shown that the relaxation time for a magnetic domain will increase exponentially as the temperature is lowered. Thus some grains which are SPM at room temperature (≈300K) will behave as single domains capable of retaining remanence at much lower temperature. Conversely, any net remanence held by these domains at low temperature will disappear as they warm in field-free space across their SPM/SD transition (their blocking temperature). For the first warming cycle, the sample was given an IRM at low temperature, and the magnetization then monitored through time (curve 1) as the sample warmed inside the field-free region of the magnetometer. Then, curve 2 was obtained after the sample has been cooled down, but not given an IRM. Curve 3 shows a subsequent warming cycle following the same procedure as for the first cycle. See text for more details. The progressive decrease in curves 1 and 3 compared to curve 2 suggests the presence of SPM ferromagnetic grains in the newt.

Our magnetometry results, along with the fact that ferromagnetic material found in animal and human tissue was mostly identified as the iron oxide magnetite, suggest that SD/SPM magnetite particles are the most plausible magnetization carrier in the Eastern red-spotted newt (*Notophthalmus viridescens*). This remains, however, to be confirmed by extraction and clear characterization (using e.g. transmission electron microscopy and electron diffraction).

This is the first time a ferromagnetic material has been detected in an amphibian. More interestingly, this amphibian has the ability to rely on the Earth's magnetic field for orientation (e.g., Phillips, 1986b). Regardless of the debate about the compass mechanism which still requires other kinds of biophysical, behavioral and neurophysiological data to resolve, the presence of such a material in the Eastern red-spotted newt represents a important element regarding the navigation system of this animal. Indeed, the newts have been demonstrated to display true navigation after being deprived of magnetic, visual, olfactory and inertial cues during displacement from their home pond (Phillips et al., 1995). Given that in this case no route-based directional information is available to them, it suggests that they are able to utilize at least a bicoordinate map. Following their findings, Phillips and Borland (1994) suggested that the geomagnetic field plays a role in this map. And new results from a recent study (Fischer et al., in preparation) yield direct experimental evidence for the use of one component of the magnetic field (i.e., inclination) in the map step of homing by newts. Yet an important requirement of a system deriving map information from the geomagnetic field is a high level of sensitivity (Gould, 1980; Moore, 1980). The radical pair recombination mechanism that could be involved in part of the newt's orientation behavior (Phillips and Borland, 1994) does not provide this kind of sensitivity (Schulten, 1982), whereas a system based on a ferromagnetic material such as magnetite theoretically could (Kirschvink and Walker, 1985). This latter would also be compatible with the magnetic polar discrimination the newts display when homing is experimentally elicited (Phillips, 1986b). It is thus critically important that the location and functional properties of the ferromagnetic material be unambiguously assessed, as this information may have a dramatic impact on our understanding of the geomagnetic field's involvement in the navigation system of the newt.

In conclusion, magnetic sensitivity has been shown in a large number of animals (for a review see e.g. Wiltschko and Wiltschko, 1995). But with the possible exception of the rainbow trout (Walker et al., 1997), the search for magnetosensitive cells has been frustrating. Our study reveals the existence of a ferromagnetic biomineral in the Eastern red-spotted newt's body. This is the first direct evidence for the presence of ferromagnetic particles in an amphibian, thus expanding the variety of animal species containing such materials. Its magnetic properties are consistent with a SD/SPM grain-sized material belonging to the maghemite-magnetite family, thus in accordance with the "hybrid mechanism" hypothesis (Phillips and Borland, 1994). However, though theoretical considerations associated with our results and behavioral data now make of magnetite the best candidate for the putative magnetoreceptors involved in the map component of homing of this amphibian, any full interpretation needs the clear spatial and structural characterization of this ferromagnetic biomineral.

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