How ants use the ocelli to detect the polarized light in the sky is a matter for speculation. We know from intracellular electrophysiological recordings that all photoreceptors of the *Cataglyphis* ocelli are ultraviolet receptors and that they are highly sensitive to polarized light (*12*), but it would be premature to design models of E vector detection until much more is known about how the analyzer directions of the photoreceptors are spatially arranged within the retina and how the photoreceptor axons converge onto the first-order interneurons (*13*). Electrophysiological measurements have shown that the ocelli of *Cataglyphis* look at regions of the sky that are closer to the horizon than to the zenith and that within the horizontal plane the visual axes of the left and right lateral ocelli deviate by 90° from the visual axis of the median ocellus (*14*). The ant's ocelli might then be thought of as a three-detector system that scans the sky for compass information. A scanning strategy involving widely separated detectors would correspond well with the striking behavior of ants in which the compound eyes have been occluded: the continual sideways movements resulting in tortuous walking trajectories.

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10. For distances of more than 1 m from the start, the directions of the ants' mean orientation vectors are always significantly different from the direction of the spot of polarized light [$P < 0.01$, Watson-Williams test on page 95 in E. Batschelet, *Circular Statistics in Biology* (Academic Press, London, New York, 1981) used for varying azimuth positions of the spot of polarized light] (Fig. 1C). Thus, phototactic responses that occasionally occur toward the spot of polarized light do not at all govern the response. Furthermore, the ants do not take the spot of polarized light for a point lying along the solar or antisolar meridian (Fig. 2C) [$P < 0.01$, Stephens test in E. Batschelet, *Statistical Methods for the Analysis in Animal Orientation and Certain Biological Rhythms* (American Institute of Biological Sciences, Washington, D.C., 1965), p. 29].
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## Temperature Acclimation: Improved Sustained Swimming Performance in Carp at Low Temperatures

Abstract. *At low temperatures, the reduction in mechanical power output of the aerobic muscle forces cold-blooded animals, such as carp, to recruit their rapidly fatiguing anaerobic fibers at relatively slow swimming speeds. Previous experimental data have suggested that changes in the biochemistry and morphology of the aerobic muscle during cold acclimation might increase its output of mechanical power. The present experiments show that, because of these changes, carp can swim faster at low temperature using only their aerobic muscle, which results in an increase in their sustainable swimming speed. By modifying their musculature, cold-blooded animals can achieve some independence from the effects of seasonal changes in environmental temperature.*

Cold-blooded animals must generate the same mechanical power to locomote at a particular velocity irrespective of temperature (*1*), even though the maximum mechanical power that their muscle can generate decreases by a factor of two or three with each decrease of 10°C in muscle temperature (*2, 3*). We have shown that carp compensate for this loss of mechanical power by recruiting more muscle fibers and faster fiber types at low temperature (*1*). The neural mechanism appeared to be a "compression of the recruitment order" over a narrower range of swimming speeds at low temperature (*1*). The carp seemed to recruit motor units in the same order at low and high temperature; for example, at low velocities only the aerobic (red and pink) fibers were recruited, and as swimming velocities increased, the anaerobic white fibers were recruited as well. At low temperatures (10°C), however, the carp recruited all their aerobic red and pink fibers over a relatively small range of swimming velocities (15 to 26 cm/sec), whereas at 20°C the fibers were recruited over a greater range of velocities (15 to

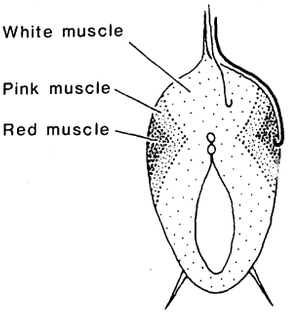


Fig. 1. Placement of the EMG electrodes. The three different muscle fiber types of the carp—white, red, and pink—are segregated into anatomically separated zones (cross-sections not drawn to scale). Fish were anaesthetized, and bipolar electrodes (teflon-insulated stainless steel wire, 75 μm in diameter) were implanted in the red muscle (heavy line) and white muscle (thin line), one set below the dorsal fin and the other 3 cm anterior to the caudal peduncle (See Fig. 2). These electrodes and a ground electrode placed intraperitoneally on the fish's ventral surface were brought forward to the first spine of the dorsal fin, where they were sutured and glued in place.

46 cm/sec). To swim faster at either temperature, the carp had to recruit their fast-contracting, anaerobic white muscle.

Although the compression of the recruitment order at low temperatures enabled carp to generate the mechanical power that they needed to swim, the speeds at which they could sustain locomotion were reduced because the recruitment of the anaerobic white muscle was always accompanied by rapid fatigue. During long-term acclimation to cold temperature, however, the total mechanical power of the aerobic muscle

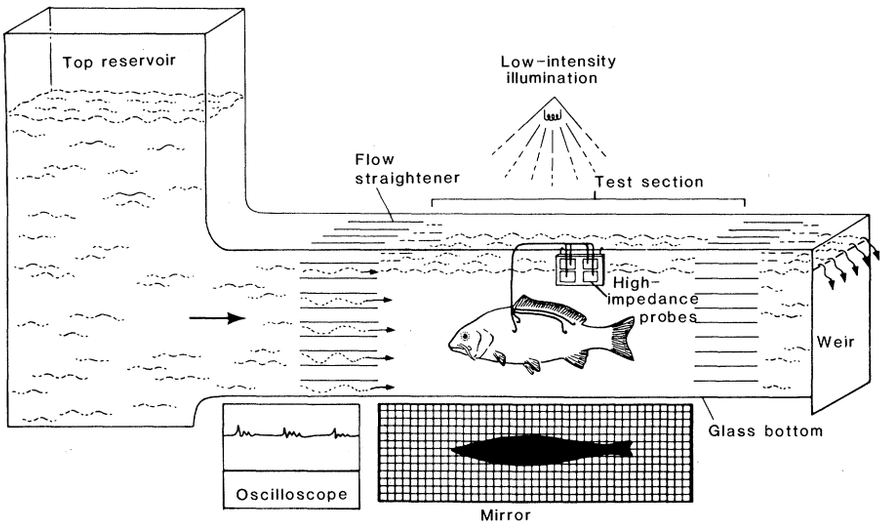


Fig. 2. Apparatus for recording EMG's and swimming movements of carp. The fish were induced to swim steadily in the central portion of the test section—where the flow was straight, constant in velocity, and non-turbulent—by illuminating the sides and back of the test section with bright lights (not shown), which they avoided. For acquiring the best EMG signals, the unshielded EMG electrodes were kept as short as possible by connecting them to high-impedance probes mounted onto the side of the flume. To exclude periods of acceleration and unsteady swimming from our analysis, we simultaneously recorded the fish's movements and EMG's. The fish's silhouette (formed by low-intensity back-lighting and projected through the glass bottom onto a mirror inclined at 45°) and its EMG's (displayed on a large-screen oscilloscope) were filmed with a video camera. The EMG signals were also recorded on the audio tracks of the video recorder.

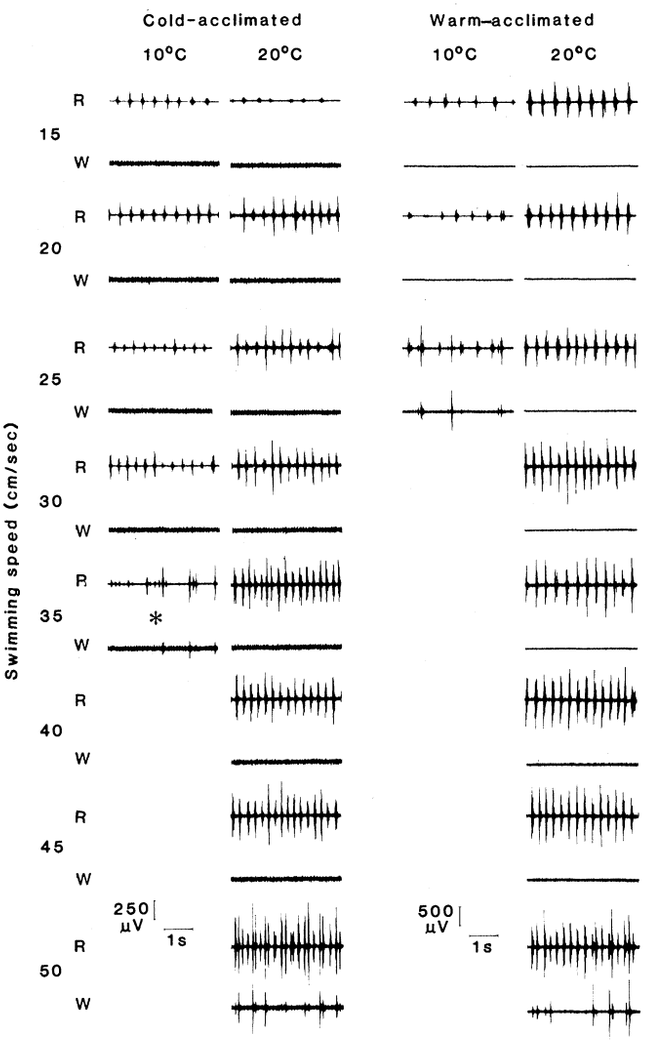


Fig. 3. Electrical activity of red (R) and white (W) muscle during swimming at different speeds and temperatures in cold- and warm-acclimated carp. Fish 4 (cold-acclimated, 8°C) was first induced to swim at 10°C and 48 hours later at 20°C. Fish 6 (warm-acclimated, 26°C) was first induced to swim at 20°C and then at 10°C. After implantation of electrodes, each animal was allowed to recover for 24 hours. The fish were then allowed to swim at a low speed for several hours before any measurements were made. At low speeds, only bursts of red muscle activity were observed, each of which corresponded to a tail beat. At higher speeds the white muscle was recruited as well. The swimming velocity at which white muscle was initially recruited was estimated to be the average between the speed at which white muscle activity was first observed and the speed immediately below it. (*) The EMG records at 10°C for fish 4 were taken at 33 cm/sec. At swimming speeds faster than those at which white muscle was initially recruited (not performed by these fish), the white muscle is recruited more frequently, and the amplitudes of the EMG's are larger than those shown. The amplitudes of the white muscle EMG's were correlated to the speed and amplitude of the tail movements and to the resulting acceleration of the fish. Presumably, the magnitude of the EMG's was proportional to the number of simultaneously active muscle fibers. The magnitude of the electrical noise on the EMG channels was originally 20 μV (*1*), but multiple stages of editing the video tapes appear to have increased the noise to approximately to 60 μV. However, this additional electrical noise did not obscure electrical activity of the muscle.

may be increased in carp by an increase in the maximum output of mechanical power per gram of aerobic muscle (*4*) [the rate of myofibrillar adenosine triphosphatase (*5, 6*)] and by an increase in the volume of the aerobic muscle (*6*). We now describe our electromyographic (EMG) study showing that, as a result of cold acclimation, carp can swim faster with their aerobic muscle and thus have a higher sustainable swimming speed.

The carp (*Cyprinus carpio*) were divided into two groups; one group was kept at 8° ± 1°C and the other at 26° ± 1°C for 2 months before experimentation. Bipolar EMG electrodes were placed in the red and white myotomal muscle as described (*1*) (Fig. 1), and the fish were made to swim steadily in a flume at various speeds at 10° and 20°C while their EMG's and swimming movements were recorded simultaneously with a video system (Fig. 2).

As has been reported (*1, 7, 8*), the red fibers were active at slow swimming velocities, and the white muscle was not recruited until the velocity of swimming increased (Fig. 3). There was no evidence to suggest that red muscle activity ceased at high speeds nor that white muscle was recruited at low speeds. By careful analysis of the videotapes, we determined the initial velocity at which white muscle was recruited as that at which the fish were no longer able to maintain their position in the flume for ten tail beats without recruiting their white muscle. The velocity at which white muscle was initially recruited varied depending on the temperature to which the fish were acclimated and on their muscle temperature during the test.

At 10°C, white muscle was first recruited in the warm-acclimated fish at a swimming speed of approximately 22 cm/sec, whereas the cold-acclimated fish could swim at a speed of approximately 31 cm/sec before recruiting their white muscle (Table 1). An intermediate speed of 26 cm/sec has been determined for fish acclimated to 15°C (*1*). Because these three values are statistically different from one another ($P < 0.02$), it appears that the velocity at which white muscle is initially recruited becomes higher as the acclimation temperature is reduced. This results in a lowering of the $Q_{10}$ value for the effect of temperature on sustainable swimming speed from 2 to about 1.4. The extent of the acclimation can be appreciated by considering that the difference between swimming speeds for the cold-acclimated and warm-acclimated groups represents a 2.4-fold increase in power output of the aerobic muscle [the power difference between these two swimming velocities ($V$) is given by $V^{2.5}$ (*9*)]. However, the compensation is not complete, and temperature still has an effect on sustainable swimming performance.

Table 1. Speed of initial white muscle recruitment as a function of muscle temperature and acclimation temperature.

| Fish | Swimming velocity (cm/sec) | |
|---|---|---|
| | 10°C | 20°C |
| *Cold-acclimated (8°C)* | | |
| 1 | 28 | 43 |
| 2 | 33 | 48 |
| 3 | 33 | 43 |
| 4 | 32 | 48 |
| 5 | 28 | 38 |
| Mean ± S.E.M. | 30.8 ± 1.2 | 44 ± 1.9 |
| *Warm-acclimated (26°C)* | | |
| 6 | 23 | 48 |
| 7 | 21 | 38 |
| 8 | 21 | 38 |
| 9 | 22 | 48 |
| 10 | 22 | 43 |
| Mean ± S.E.M. | 21.8 ± 0.4 | 43 ± 2.2 |

Although the swimming velocity at which white muscle was initially recruited at 10°C was dependent on acclimation temperature, the velocity at which white muscle was initially recruited at 20°C was the same in all acclimation groups: 44 cm/sec for the group acclimated to 8°C, 43 cm/sec in the 26°C group, and 46 cm/sec for the 15°C group (*1*). Several factors might contribute to this result. First, although the output of mechanical power from the aerobic muscle of the cold-acclimated fish was higher than that of the warm-acclimated fish at low temperatures, at high temperatures measurements of myofibrillar adenosine triphosphatase (*10*) suggest that the outputs may be similar. Second, there is evidence that the nervous system of animals acclimated to low temperatures limits locomotory performance at high temperatures to a level well below the capabilities of the muscle (*11*). For instance, in frogs, where modification of muscles does not occur during acclimation (*3, 12*), the jumping capability of cold-acclimated (5°C) frogs falls to less than 50 percent of that of the warm-acclimated (25°C) frogs when measured at 20° and 25°C, even though the animals have the same jumping capabilities between 5° and 15°C (*13*). This may be due to the nervous system of the cold-acclimated animal being incapable at high temperatures of recruiting all the motor units or of recruiting the motor units in the temporal sequence necessary for the generation of maximum power. Third, the reduced availability of oxygen at high temperatures may make the respiratory and circulatory systems of the carp unable to support metabolically the increased power production of the extra oxidative muscle tissue at 20°C. It seems, therefore, that this type of adaptation is particular for cold temperature swimming, because the differences in performance are noticeable at the cold temperatures.

Taken together with the biochemical (*5, 6*), physiological (*4, 14*), and histochemical (*6, 7*) aspects of the acclimatory changes, our findings reveal one of the ways in which poikilotherms gain some independence from environmental temperature over a period of a few weeks. The increase in myofibrillar adenosine triphosphatase (mechanical power output) in species such as the carp, trench (*15*), and roach (*15*), along with an increase in the number of red fibers during low-temperature acclimation, enable these species of fish to derive more power by aerobic means and hence to avoid long recovery periods associated with anaerobic metabolism. This form of acclimation, however, is not universal, since neither the mechanical power of frog muscle (*3, 12*) nor the jumping ability of frogs is enhanced by long-term exposure to low temperature (*13, 16*).

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