Physiological Adaptation to Cold of Peripheral Nerve in the Leg of the Herring Gull (Larus Argentatus)

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Measurements made by one of us (L. I., unpublished) have indicated that the internal temperature of the uninsulated metatarsal portion of the leg of a subarctic Alaskan gull (Larus glaucescens) is near 0°C in an environmental temperature of −10° to −30°C, while in the well-feathered tibial parts of gulls' legs the temperature of the tissue is approximately that of the body. It was thought possible that the peripheral nerve in the metatarsal part of the leg might show an adaptation to function in cold not possessed by more proximal segments of the nerve which are protected by the feathers and muscles of the tibial and femoral parts of the leg. To test this hypothesis we have investigated conduction in excised superficial peroneal nerves of herring gulls (Larus argentatus) as a function of temperature. The gulls examined had been wintering on the coast of Maine in temperatures but little warmer than the environment of their Alaskan relatives. Their nerves were found to show a gradient in resistance to cold, the more distal segment conducting at much lower temperatures than did the more proximal. The prominence of this gradient was directly related to the coldness of the environment in which the birds had been experimentally maintained. The functional resistance to cold in the nerve from the metatarsus is thus the result of some process of adaptation which occurs during exposure to low temperatures.

A comparative study was made using the homologous nerve from the leg of the domestic hen (Gallus domesticus), the metatarsal portion of which remains warm even at low environmental temperatures. This fact may be correlated with the different structure of the hen’s leg, which is feathered well down on the metatarsus, proportionally larger in diameter, and fleshier. Little or no gradient in the resistance to cold was apparent in the hen nerves.

Materials and Methods

Full-grown herring gulls (L. argentatus), some still in juvenal plumage, were studied. They were divided into three groups. One group (henceforth called the ‘cold adapted group’) was maintained in a cage at an environmental temperature of −10° to 0°C from the time they were captured in midwinter until they were killed more than 3 weeks later. A second group (hereafter referred to as the ‘warm adapted

Received for publication November 21, 1952.

1 This research was supported in part by the Milton Fund of Harvard University and in part through Air Force Contract No. AF33(658)-18133.

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3 We are greatly indebted to Dr. G. Edgar Folk, Jr., Department of Biology, Bowdoin College, Bowdoin, Maine, who arranged to supply us with gulls captured by members of the Department of Sea and Shore Fisheries of the State of Maine.
group') was kept at a room temperature of 26–30°C. for over a month before the experiments were performed. The warm adapted group was kept in a cage which contained two pans, one filled with salt water maintained at room temperature, and the other running fresh water with a temperature varying between 26° and 40°C. The gulls spent about an equal period of time with their feet immersed in one or the other of the two pans which they seemed to prefer to the bare floor of their cage. A third or 'heat adapted group' was maintained at an environmental temperature of 24–35°C. for 14 to 28 days before the experiments were performed. The 'heat adapted' birds were kept in a cage whose floor consisted of a flat pan filled with fresh water at 37°C. to a depth of 11 cm. so that the metatarsal portions of the gulls' legs were continuously immersed.

The hens studied were obtained from dealers or local farms and were maintained before death at the ordinary room temperature of the laboratory. Thus they were comparable to the 'warm adapted' group of gulls.

At the time of study each bird was removed from its cage and the temperature of the metatarsal (tarso-metatarsal) and the tibial (tibio-tarsal) portions of the leg and the deep abdominal temperature quickly taken with an iron-constantan needle thermocouple. Every effort was made to record the leg temperature before such factors as handling the bird could cause a change, and the temperatures were always measured at the environmental temperature to which the bird had been exposed. It was assumed that the metatarsal temperature of the birds standing in the hot water would be at least as high as the temperature of the water itself and no effort was made to measure temperature of the legs while they were submerged.

A Micromax thermoelectric recorder, calibrated to ±0.5°C. was used for all temperature measurements. After these measurements, the bird was killed by a blow on the head and the superficial peroneal nerves were excised. The part of the nerve which was dissected from the metatarsal portion of the leg was studied separately from that which came from the tibial part. Each nerve to be studied was mounted on silver wire electrodes in a sealed lucite chamber which was in turn placed in an insulated box, the temperature of which could be controlled by means of a heater and a refrigerating unit. The nerve was left at a given temperature for at least 4 minutes before any observations were made. The temperature inside the lucite chamber was measured with a thermocouple. The nerve was stimulated with a Grass stimulator and the action potentials recorded photographically on a cathode ray tube face after the usual differential amplification. If the action potential was just visible at a given temperature but absent when the nerve was next stimulated at a lower temperature, the nerve was considered to have ceased conducting midway between the two observed temperatures. In all, 40 segments of nerve from 11 gulls and 14 segments from 9 domestic hens were studied.

4 The nerves used were initially identified in hens by reference to Kaupp's Anatomy of the Domestic Fowl (Philadelphia and London: Saunders, 1918). Homologous nerves were then dissected from gulls.
ADAPTATION TO COLD

RESULTS

Comparisons of Deep Abdominal, Tibial and Metatarsal Temperatures of Hens and ‘Heat Adapted’, ‘Warm Adapted’ and ‘Cold Adapted’ Gulls. Table 1 shows the range of the results of measurements of deep abdominal, tibial and metatarsal temperatures in the three groups of gulls and in domestic hens. It will be noted that the temperature of the metatarsus of the ‘heat adapted’ and ‘warm adapted’ gulls was lower than both the environmental temperature and the temperature of the wading pans. This was undoubtedly due to evaporation of water from the wet skin of the leg during measurement.

The variations in temperature which we recorded are typical of birds in general, as Baldwin and Kendeigh (1) have emphasized.

It is apparent from table 1 that, in gulls, the environmental temperature has a profound effect on the temperature of the unfeathered, metatarsal portion of the leg without significantly affecting the deep abdominal or tibial temperature. We believe that this sharp temperature difference between the tibial and metatarsal portions of the leg is of importance in bringing about the apparent adaptation to cold which we have found in the peripheral nerve of the gull and which we shall describe below. In the well-feathered leg of the hen, the difference in temperature between the tibial and the metatarsal regions is relatively small compared to the gull.

Differences in the Temperature Sensitivity of Tibial and Metatarsal Parts of the Superficial Peroneal Nerve. Figure 1 shows the temperatures at which conduction ceased when distal and proximal segments of nerve from the three groups of gulls and from hens were cooled. The metatarsal portion of the excised peroneal nerve of the gull was more resistant to cold than that from the tibial portion. Furthermore, this difference was much greater in the cold adapted group and less in the heat adapted group than in the warm adapted gulls. Whether adapted for 2 weeks or a month, the nerves of all heat adapted gulls showed the same loss of resistance to cold. Little or no difference in resistance to cold was apparent between the metatarsal and tibial portions of the nerves of hens as a group, as figure 1 reveals, although in individual hens there was a tendency for the metatarsal segment to conduct at slightly lower temperatures than the tibial segment. The metatarsal portion of the hen’s nerve never conducted at the low temperatures at which the cold adapted gull’s nerve might still be functioning. In this relation to temperature the hen’s nerve resembled that of the ‘heat adapted’ gulls.

Figure 2 illustrates a representative experiment, showing the nerve action potential of a ‘cold adapted’ gull at various temperatures. In this nerve the tibial
portion ceased to conduct at 11.7°C, while the metatarsal part conducted until cooled to 2.8°C. In all experiments the blocking by cold was reversible.

As the nerves were cooled, the excitability, measured as the reciprocal of the stimulating voltage which just sufficed to bring the fibers of lowest threshold into activity, decreased linearly with temperature. The conduction velocity of the fastest fibers, which in the gull nerves studied was about 25 m/sec at 38°C, also decreased linearly with temperature, usually more rapidly in the tibial portion of the nerve than in the metatarsal part. The height of the compound action potential, which

![Diagram](https://example.com/diagram.png)

Fig. 2. Typical action potentials of gull's superficial peroneal nerve at various temperatures as indicated. On the left, the action potential of the metatarsal portion which was still present at 3.9°C but not at 2.8°C. On the right, action potential of the tibial portion which was present at 14.4°C but absent at 11.7°C.

Fig. 3. Conduction velocity and height of the action potential of the two portions of the nerve of figure 2 plotted against temperature. Conduction velocity decreased linearly with temperature. The height of the action potential passed through a maximum which was different in the two cases.

was dependent both on the size of individual spike potentials and on the amount of their temporal dispersion produced by cooling, passed through a maximum at some intermediate temperature. This maximum was at a lower temperature in the metatarsal portion of the nerve from gulls but not in that from hens. The relation to temperature of the conduction velocity and the height of the action potential of the gull nerve whose action potential is shown in figure 2 is graphed in figure 3.

The compound action potential in the nerves studied frequently showed two or more components. In figure 3 the change in conduction velocity of the fastest component only has been plotted.

An incidental observation was that nerves from hens conducted at rates up to 100 m/sec, which was considerably faster than the maximum conduction velocity of gull nerve.
DISCUSSION

It is perhaps not surprising that peripheral axons should show quantitatively different properties along their length since Rosenblueth and del Pozo (2) have described gradients along mammalian nerve in its susceptibility to Wallerian degeneration, and Groat and Koenig (3) have shown that gradients exist in the susceptibility of peripheral nerve to asphyxia. None of these changes, however, has been shown to be adaptive to a changing environmental condition.

The resistance to cold of nerve in the metatarsus of the gull is an obvious adaptation to the temperature of the leg and to the cold environment in which the bird generally finds itself. Wetmore (4) pointed out that the feet and tarsi of some birds are often cold in spite of their high body temperature. Apparently, however, the temperature of the metatarsal part of the legs of birds varies between species. Thus, we have found in this study that the legs of domestic hens have relatively high temperatures even in a cold environment, a condition which also exists in the raven, Corvus corax principalis (5). On the other hand, the temperature of the legs of gulls can drop to near freezing. Arteriovenous anastomoses have been described in the feet of many birds (6, 7), and as Scholander, Walters, Hock and Irving (8) have shown in arctic birds such as the gull, the circulation to the leg must require rather delicate control to conserve heat and at the same time to keep the metatarsal and foot temperature from reaching freezing levels. In addition Strong (9) and Madsen (10) have pointed out that northern gulls often cover their bare legs and feet by squatting on them while resting on ice or snow during cold weather. This postulates that the nerves in the metatarsal portion of the leg are functioning at temperatures near 0°C.

It also seems probable that, under natural conditions, the temperature of the metatarsus of the herring gull rarely approaches the body temperature. Certainly the metatarsal temperature was not even as high as the environment in gulls which had been maintained in a heated room and had waded in warm water. It is interesting that extremely cold weather has no apparent deleterious effect on the feet of gulls, while hens with their relatively warm legs frequently suffer from frozen feet. Scholander et al. (8), however, observed that a gull kept in a warm room froze the web on its feet when it happened to escape into a cold environment, which may be an example of loss of the adaptation apparent from our experiments.

In a previous publication from these laboratories (11) it was pointed out that peripheral nerves of animals capable of hibernation were more resistant to cooling than the peripheral nerves of homeotherms. But in animals which can hibernate, in contrast to our findings on the gull, the resistance does not depend upon the previous environmental temperature or upon whether the nerve is taken from an animal which is actually in hibernation; it is a constant, innate difference, independent of the animal's previous history and physiological state at the time.

The acquired resistance to cold which we have observed in gull nerve is reminiscent of the physiological differences in muscle metabolism and cardiac function between 'summer' and 'winter' frogs (12, 13) but it is questionable whether such observations can be helpful in understanding the problems of cold adaptation in homeotherms. Just what property of the nerve (e.g. the membrane potential) may be affected, how this change is brought about and the temporal course of the phenomenon of adaptation are problems that are now opened for future research.5

5 Dr. E. H. Leduc of the Department of Anatomy has used histochemical methods to compare segments of gull nerves which showed this temperature gradient. The group of tests included re-
When herring gulls (L. argentatus) are maintained in a cold environment, the internal temperatures of the metatarsal and tibial parts of the leg differ markedly, that of the tibial part being much warmer.

The resistance to cooling of peripheral nerve from the tibial and metatarsal portions of the legs of gulls was studied in vitro. It was found that nerve from the metatarsus conducted at significantly lower temperatures than nerve from the tibial portion of the leg, and that this difference was more pronounced if the gull had been kept for long periods at a low environmental temperature which resulted in a lowering of temperature in the metatarsus, and least pronounced in gulls forced to wade in a pan of water at 37°C. This resistance to cold was not observed in nerves from domestic hens, whose legs differ in structure and do not show the temperature gradient found in the legs of gulls.

Nerves from gulls conducted at a maximum velocity of about 25 m/sec.; those from hens at a maximum velocity of 100 m/sec. On cooling the gull nerves, there was a linear decrease in excitability and conduction velocity, whereas the height of the compound action potential passed through a maximum which occurred at a lower temperature in the nerve from the metatarsal portion of the leg than in that from the tibial part.

It is pointed out that other differences have been found in properties along peripheral nerve. Furthermore, species differences exist in the resistance of nerves to cold. The exact mechanism and temporal course of the adaptation to cold of the peripheral nerve of the herring gull remain to be studied. Histochemical study did not reveal any differences in chemical morphology between tibial and metatarsal portions of the nerves.

We wish to thank Miss Doris Chambers for her technical aid and for her correlation and analysis of the data.

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actions for succinic dehydrogenase, acid phosphatase, aliesterase, carbonyl groups, lipids and carbohydrate-containing compounds. No differences were detected between the tibial and metatarsal portions of the nerves.