in humans and animals after damage to the AV nucleus and related structures (*13*).

Finally, we hypothesize that the late-forming neuronal discrimination relayed from the AV nucleus back to the superficial laminae may inhibit ongoing neuronal discrimination acquired in the deep laminae in the early stages of acquisition. Thus, once neurons of the AV nucleus are able to produce their own discriminative activity, feedback from the AV nucleus may promote disengagement of the cingulate cortex from the discrimination process.

Two sources of evidence suggested such disengagement. First, 19 of the 22 cortical records that indicated acquired neuronal discrimination at early stages of behavioral acquisition showed its loss in the late stages. Second, only neurons in the AV nucleus manifested reversal of the original discriminative activity during behavioral reversal training (*7*). Thus, relegation of the discriminative response by neurons in the deep laminae to the AV nucleus may free the deep laminae to process new discriminative problems.

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Interaction Between Posture, Color, and the Radiative Heat Load in Birds

Abstract. *The effect of the angle of incidence on the radiative heat load was determined for light and dark plumage. As the angle of incidence to the solar radiation source increases the difference in heat transfer between light and dark plumage disappears. Thus, by postural adjustment, a dark bird may become thermally white with regard to the radiative heat load.*

Cartwright and Harrold (*1*) proposed that plumage coloration could be important to thermal regulation in birds, since color should influence the absorptivity of solar radiation. Several investigators (*2*, *3*) have conducted metabolic studies in the laboratory to show that birds when below thermal neutrality can use solar radiation to allieviate thermal stress. Monteith (*4*) pointed out that "reflectivity is an important discriminant in the heat balance of animals but the relationship between coat color and radiative heat load is complex." There is still a question as to whether dark or light plumage is more effective in the utilization of direct solar radiation. Several studies (*2*, *5–7*) have shown dark coloration to be more effective in the use of solar radiation, while others (*8*) have shown light coloration to be more effective in radiative heat gain. Further, convective cooling (*9*) differentially affects the radiative heating of dark and light plumages, so that at low wind speeds black plumages acquire a greater radiative heat load than do white plumages, but the heat loads of black and white plumages rapidly con-

Table 1. Heat flow through feathers as a function of color, angle, and air temperature; G, gray; W, white.

T_a (°C)	Color	W m^{-2}	T_{skin} (°C)	T_r (°C)*	$T_{surface}$ (°C)	N
			90° angle			
27.0	G	119.1 ± 10	40.0	37.3	69.7	3
27.0	W	61.2	39.5	37.6	62	2
20.0	G	102.6 ± 11	40.2	36.7	69.5	4
20.0	W	46.0 ± 10	38.8	37.0	57.2	4
20.0†	G	54.6	39.5	36.5	67	2
20.0†	W	14.5	36.7	36.5	48.5	2
10.0	G	71.0 ± 5	38.5	36.6	62	3
10.0	W	35.5	38.2	36.5	49.5	2
			135° angle			
27.3	G	50.6 ± 6	38.4	37.0	52.5	3
27.0	W	32.9	38.1	37.1	43.9	3
20.0	G	33.5 ± 4	38.1	36.8	48.0	3
20.0	W	21.0 ± 7	38.1	37.1	41.0	3
20.0†	G	25.6	37.7	37.0	45.0	2
20.0†	W	9.9	36.5	36.5	36.5	2
10.0	G	10.5	36.9	36.3	44.0	2
10.2	W	7.2 ± 1	36.2	35.5	27.0	3
			160° angle			
27.9	G	21.0 ± 9	37.4	36.9	43.7	4
27.0	W	17.8 ± 5	37.1	36.8	39.5	4
20.0	G	2.0 ± 1	36.8	37.0	36.5	3
20.0	W	4.0 ± 5	36.6	36.8	35.7	4
20.0†	G	0	35.0	37.0	35.0	2
20.0†	W	0	36.0	37.0	29.5	2
10.0	G	0	35.0	36.7	32.0	2
10.0	W	0	36.4	36.5	32.0	3

*Radiation passed through 1 cm of water. †Temperature of reservoir.

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verge as wind speed is increased and feathers are erected. Not only are wind, temperature, and color important to the radiative heat load but the posture (angle of incidence) of the animal is also important (*6*). Since posture seems to be important to the energy balance of the animal, we conducted experiments to investigate the effects of posture (angle of incidence), air temperature, and color on heat flow through the plumage layer. We therefore considered the effect of posture on the utilization of direct solar radiation, and the effect of the interaction of color and posture to maintain thermal balance.

We measured the heat flow through patches of plumage taken from the breast and the back of adult herring gulls (*Larus argentatus*). The white breast plumage has an absorptivity of 15 percent while the gray back plumage has an absorptivity of 50 percent. Heat flow was monitored with a heat flow tranducer (Thermonetic) placed between the under side of the plumage and simulated bird (Fig. 1). The mean temperature of the water reservoir (T_r) within the simulated bird was 36.7° + 0.4°C. The radiation source was a clear-end infrared (General Electric) bulb (250 W). We monitored the heat flow through the feathers at three different angles (90°, 135°, and 160°) with respect to the radiation source (Fig. 1), and at three different air temperatures: 10°, 20°, and 27°C. The total radiation level was 1115.6 W m^{-2}. Of the total, 697.3 W m^{-2} was between 400 and 3200 nm. The remaining 418.3 W m^{-2} was between 3.2 and 60 μm. The radiation levels were determined by a glass-domed pyranometer (sensitive to 3.2 μm) and a polyurethane-domed radiometer with unidirectional attachment (sensitive to 60 μm). The experiment was repeated at 20°C with a centimeter of water (maintained at 20°C) between the radiation source and the plumage (Fig. 1); thus only a small amount of radiation (697.3 W m^{-2}; 400 to 1400 nm) reached the dorsal surface of the plumage. The distal ends of the feathers pointed away from the radiation source. As the angle of incidence was increased, the distance from the light source to the feather surface was maintained constant.

Prior to any experimentation, we determined the insulating quality of each plumage patch by using the heat flow transducer to monitor the heat transfer through the feather layers while they rested on a hot plate. The white plumage with a natural fluff was twice as good an insulating layer as the gray plumage with a natural fluff (23.7 W m^{-2} and 49.3 W m^{-2}, respectively). When the feather layers were compressed, the insulating values were similar (179.6 and 196.4 W m^{-2}). All experiments were conducted on plumages with a natural fluff.

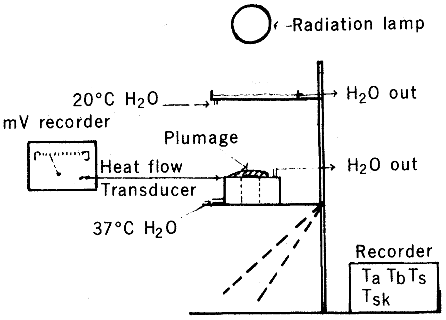

Fig. 1. Experimental setup for determining the effect of posture on radiative heat load.

In gray and white plumages receiving both short- (400 to 3200 nm) and longwave (3.2 to 60 μm) radiation (1115 W m^{-2}), the heat transfer through both feather layers declined with decreasing air temperature (Table 1). As the angle of incidence increases due to postural adjustments, there is a further reduction in heat transfer through the feather layer (Table 1). At the 90° angle the darker plumage, at each test temperature, is transmitting about twice as much energy as the white plumage (Table 1). This greater heat transfer implies a greater absorptivity; therefore, it would seem that dark color facilitates absorptivity of radiant energy. This does not hold since the insulating quality of the gray plumage was half that of the white; therefore, the gray plumage should transmit twice the energy, color not being a consideration. These data would indicate that color is of little importance in the use of solar radiation, whereas postural changes are of great importance. Yet, previous studies suggested that color was important. Since in previous laboratory studies (*3, 5, 6*) dealing with energetics, the birds received little longwave radiation (greater than 3200 nm) and longwave radiation is absorbed as if the object were a black body regardless of color, it is possible that the longwave radiation used at 418.3 W m^{-2} in this experiment masked the effect of color under natural conditions. In our field studies we found that longwave radiation from the sky ranged between 209 and 279 W m^{-2} (*7*). To test this, we repeated the experiment at an air temperature of 20°C with just 697.3 W m^{-2} of shortwave radiation (400 to 1400 nm). We still found a decreased heat flow with postural change (increased angle of incidence). When the radiation source is perpendicular to the plumage (90° angle), the gray plumage transmits four times as much heat (Table 1) as the white plumage does. Only half of this can be accounted for by the difference in insulative quality; the rest is due to color difference. It becomes obvious from these data that as the bird increases the angle of incidence to direct solar radiation through postural changes that color becomes less important. In plumages receiving shortwave radiation at 697 W m^{-2} (0.4 to 1.4 μm), as the angle of incidence increases, the reflection coefficient goes up no matter what the color. The gray plumage transmitted four times as much heat as the white plumage at a 90° angle, and 2.5 times the heat at a 135° angle; there was no significant difference in heat transfer between gray and white plumage at a 160° angle of incidence.

In considering the importance of color to radiative heat load, the bird's ability to decrease absorptivity by postural adjustments must be included, as well as stress induced by heat or cold. During heat stress a dark bird by postural adjustment (increasing the angle of incidence) can effectively become white with regard to solar radiation. A cold-stressed bird would require a large surface area at 90° to the radiation source, and under these conditions a darker color would have the greatest benefit. Thus by postural adjustments birds can decrease the effects of dark coloration under heat stress and increase its effect when cold stressed. The interaction of air temperature, solar intensity, and wind velocity induced both postural and orientation adjustments in adult herring gulls (*7*).

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