

NERVOUS CONTROL OF CHROMATOPHORES IN TELEOST FISHES

IV. A COMPARATIVE SURVEY OF LOCAL TEMPERATURE RESPONSES

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INTRODUCTION

The strong chromatic responses to local heating or cooling of the skin, found in *Phoxinus* by von Frisch (1911*b*), have been reported from few other teleosts. Von Frisch (1912) noted similar effects in the melanophores of *Crenilabrus pavo* and the erythrophores of *Trigla corax* and *T. lineata*; Smith (1928) performed similar experiments on *Fundulus heteroclitus*; Smith & Smith (1935) found the response in erythrophores of *Holocentrus ascensionalis*. No reports on any other species can be found in the literature.

The following survey was undertaken in order to see how widespread the responses are, to see if there is any variation in the response and to examine a possible correlation of the effect with the presence of rapid nervous control of normal chromatic adaptation. Background reversal was checked for each species as follows. Each test fish was placed in turn in a black or a white tank for some hours and then moved quickly to one of the opposite colour which already contained a fully adapted fish. The intensity of colour adaptation was immediately obvious and the time taken for the two specimens to become indistinguishable was measured. This method is crude and inevitably produces shorter reversal times than would be indicated by microscopical examination of the responses of individual melanophores. It does not allow for slow humoral changes of colour nor the possible presence of inactive motor nerve systems. Furthermore, the time value assigned to the asymptotic responses can give only an approximate indication of the rate of adaptation, but this was all that was required for the present purposes. The criterion of Neill (1940) was applied to these figures, i.e. that a short reversal time (of the order of minutes) indicated nervous mediation of the response.

The same fish were then anaesthetized in turn and tested for local thermal responses with a jet of warm water and with ice or crushed sea-water ice as appropriate. Melanophore responses were observed microscopically and respiratory rhythm was checked constantly. Where possible the responses of at least four specimens of each species were examined but, as no inconsistencies were found, the results given here also include those where only single specimens were available. These results are summarized in Table 1.

Strong temperature-responses are seen to be widespread but could not be demonstrated in all those species which showed quick adaptation to background colour. No responses could be found in any species which did not show quick adaptation.

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Table 1

| Classification of species | Chromatic innervation (by Neill's criterion) | Temperature responses | Number tested |
|--|--|-----------------------|---------------|
| Order Isospondyli Family Salmonidae <i>Salmo salar</i> L. | Present(1) | Present | 7 |
| Order Apodes Family Anguillidae <i>Anguilla anguilla</i> (L.) | Not demonstrated(1) | Absent | 5 |
| Order Ostariophysi Family Cobitidae <i>Nemacheilus barbatus</i> (L.) | Present | Absent | 4 |
| Family Cyprinidae <i>Phoxinus phoxinus</i> (L.) | Present(2) | Present(3) | Many |
| <i>Rutilus rutilus</i> (L.) | Present | Present | 4 |
| <i>Gobio gobio</i> (L.) | Present | Absent | 4 |
| Family Ameiuridae <i>Ameiurus melas</i> (Rafinesque) | Present(4) | Absent | 4 |
| Order Microcyprinidae Family Poecilidae <i>Lebistes reticulatus</i> (Peters) | Present(1) | Present | 4 |
| Order Anacanthini Family Gadidae <i>Pollachius pollachius</i> L. | Present | Absent | 4 |
| <i>Onos mustelus</i> (L.) | Not demonstrated | Absent | 5 |
| Order Percomorphi Family Sparidae <i>Pagellus centrodontus</i> (de la Roche) | Present | Present | 1 |
| Family Centrarchidae <i>Eupomotis gibbosus</i> L. | Present | Absent | 2 |
| Family Labridae <i>Labrus bergylta</i> Ascanius | Weak | Absent | 2 |
| <i>Crenilabrus melops</i> (L.) | Present | Present | 4 |
| <i>Ctenolabrus rupestris</i> (L.) | Present | Present | 4 |
| Family Gobiidae <i>Gobius flavescens</i> Fabricius | Present | Present | 6 |
| <i>G. minutus</i> Pallas | Weak | Absent | 6 |
| Family Callionymidae <i>Callionymus lyra</i> L. | Not demonstrated(5) | Absent | 12 |
| Family Blennidae <i>Blennius gattorugine</i> L. | Present | Present | 1 |
| <i>B. pholis</i> L. | Present | Present | 5 |
| Order Scleroparei Family Triglidae <i>Trigla lucerna</i> L. | Present(6) | Absent(7) | 3 |
| <i>T. cuculus</i> L. | Present | Absent | 1 |
| Family Cottidae <i>Cottus bubalis</i> Euphrasen | Present | Absent | 4 |
| <i>C. gobio</i> L. | Present | Absent | 6 |
| Family Gasterosteidae <i>Gasterosteus aculeatus</i> L. | Present(8) | Absent | 5 |
| <i>Pungitius pungitius</i> (L.) | Present | Absent | 1 |

Table 1 (cont.)

| Classification of species | Chromatic innervation (by Neill's criterion) | Temperature responses | Number tested |
|------------------------------------|--|-----------------------|---------------|
| Order Heterosomata | | | |
| Family Bothidae | | | |
| <i>Scophthalmus rhombus</i> (L.) | Present | Present | 3 |
| Family Pleuronectidae | | | |
| <i>Pleuronectes platessa</i> L. | Present (9) | Present | 4 |
| <i>Limanda limanda</i> (L.) | Present (10) | Present | 1 |
| <i>Platichthys flesus</i> (L.) | Present | Present | 1 |
| <i>Microstomus kitt</i> (Walbaum) | Not demonstrated | Absent | 4 |
| Family Soleidae, | | | |
| <i>Solea solea</i> (L.) | Not demonstrated | Absent | 4 |
| <i>Buglossidium luteum</i> (Risso) | Not demonstrated | Absent | 7 |

Notes: (1) Confirms Neill (1940). (2) Confirms von Frisch (1911a), Healey (1948), etc. (3) Confirms von Frisch (1911b). (4) Confirms Parker (1934) on *A. nebulosus*. (5) Contradicts Pouchet (1876). (6) Confirms von Frisch (1912). (7) Contradicts von Frisch (1912). (8) Confirms Hogben & Landgrebe (1940). (9) Confirms Schaeffer (1921). (10) Confirms Hewer (1926).

The responses were always similar to those observed in *Phoxinus* and no new response was found. Maximal pigment dispersion within the chromatophores occurred at high temperatures and aggregation at low temperatures; both responses were reversible on return to intermediate temperatures.

There appears to be little taxonomic significance in the distribution of these results. Six species of three families of the Scleroparei all showed evidence of rapid background adaptation with no temperature-responses, although two species of *Trigla* (one of which was re-investigated here) were stated by von Frisch to show normal temperature responses. One other contradiction with the literature was found. Pouchet (1876) included drawings of both dark-adapted and light-adapted specimens of *Callionymus lyra* together with the local dispersion produced by section of the trigeminal nerve. But of six immature and six adult fish examined at Plymouth in January, none showed the slightest chromatic response to background colour, nor did two specimens darken after section of the spinal cord at an anterior level. This was later confirmed by Kent (personal communication), who was unable to induce darkening by peripheral nerve-section in this species. Further investigation of these cases is obviously necessary; possibly they represent regional, racial or seasonal variations of activity.

The families Cyprinidae, Labridae, Gobiidae and Pleuronectidae each contain some members with, and others without, the thermal response. The families Gadidae and Pleuronectidae also contain members with clear evidence of chromatic nervous control and one member in which this could not be demonstrated.

Dependence of the high-temperature response upon normal respiratory rhythm was observed in *Pagellus centrodontus*, *Ctenolabrus rupestris*, *Scophthalmus rhombus* and *Pleuronectes platessa*. The low-temperature response was found to be similarly dependent in *Ctenolabrus rupestris*. In all cases these effects were brought about by accidental overdoses of anaesthetic (Pye, 1964) from which all specimens were resuscitated with immediate resumption of normal responses.

Cessation of thermal responses following chromatic-motor nerve-section at various levels was recorded in *Pleuronectes platessa*. Darkening after section of the spinal cord

was observed in *Labrus bergylta* and *Gobius minuta*, and a slight effect was produced by section of spinal-nerves in *Buglossidium luteum*, although none of these species showed any evidence of rapid background adaptation. Similar darkening could not be induced by section of the spinal cord in *Callionymus lyra*, nor by section of spinal-nerves in *Microstomus kitt* or *Solea solea*.

Some or all specimens of *Rutilus rutilus*, *Ctenolabrus rupestris*, *Blennius gattorugine* and *B. pholis* failed to produce an immediate aggregation to the application of ice or of crushed sea-water ice. A few minutes after removal of the ice, however, the underlying melanophores aggregated completely and a little later redispersed to their former state. It is thought that this represents complete inactivation by sudden subjection to too low a temperature, followed by a reversible low-temperature response as the tissues slowly warm towards room temperature. The sequence was always repeatable.

Further experiments were performed on *Ctenolabrus rupestris*, using a cold-jet apparatus filled with sea water. This produced the normal reversible aggregation response over a range of 2–3° C. Further cooling beyond the threshold produced no further change. But, if the jet were run as cold as possible (about 0° C.) before being applied to the skin, the melanophores retained their normal appearance when cooled. Then, on slowly raising the temperature, aggregation occurred some degrees below the previously measured threshold temperature and finally, as the threshold was passed, redispersion occurred to the former state. This supports the above conclusions. It was also found that, in contrast to the high-temperature response of *Phoxinus* (Pye, 1964) the cold threshold temperature of *Ctenolabrus* showed a progressive shift throughout every experiment. Immediately after anaesthetization in urethane the threshold was generally about 6° C., but it gradually rose until, after 60–90 min., it reached room temperature. The fish then remained maximally pale and no further cold responses could be obtained. Fish anaesthetized in urethane and not subjected to temperature testing similarly showed complete blanching within an hour and a half.

These results confirm and slightly extend those obtained earlier on *Phoxinus*. They also show that temperature responses are not restricted to the few species previously examined. The effect is widespread among those teleosts that show rapid background adaptation, but it is not a necessary corollary of this. Finally attention should be drawn to the many attractive features of some of these species for studying various aspects of colour change. Most have been observed here for the first time and would be sure to repay further examination. Further information on their chromatophore patterns and responses may be found in a thesis which includes a more detailed account of this work (Pye, 1961).

SUMMARY

1. The rate of chromatic adaptation to background colour has been examined briefly in thirty-three species of teleost fishes (from nineteen families, eight orders) to test the presence of nervous control of chromatophores.

2. The same fishes have then been tested for chromatic responses to local heating or cooling of the skin.

3. Thermal responses resembling those of *Phoxinus* have been found in fourteen species which show quick adaptation, but not in thirteen other such species. No thermal responses have been found in any of the six species which do not show quick adaptation.

4. There appears to be no significance in the taxonomic distribution of these results and no new responses to temperature have been found.

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