THE PHOTOTROPIC MECHANISM IN RANATRA.

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The theory of the phototropic movements of typical insects, as proposed by Loeb (*cf.* Loeb, 1918), has conceived that forced orientation under the influence of light is due to the effect of asymmetrical sensory excitation upon the postures of opposed appendages. Asymmetrical posture of locomotor organs, resulting from forced asymmetrical stimulation of the eyes, was adequately described by Holmes (1905; 1908) and by Garrey (1917; 1918-19) for various arthropods. The respective rôles of the *rapidity of leg movements* and of the *postures of the legs*, during the course of orientation by light, have, however, never been made clear. The fact that an experienced observer (*e.g.* Mast, 1923-24) can at this late date make an inexcusable confusion between *tonic* effects determining limb posture and the *frequency* of leg movements shows that the point here raised is especially worth settling by means of a crucial case.

This particular instance is regarded as crucial because it is possible to determine by inspection the significance of limb posture in effecting orientation. The differential tonic actions of light in the case of the "water scorpion," *Ranatra*, were described some years ago by Holmes (1905). Among other things, Holmes described the "circus movements" of *Ranatra*; unfortunately, the experiments were made with horizontal illumination, and such conditions are unsuitable. If one eye of a *Ranatra* be occluded, or removed, the animal continues for hours to circle toward the remaining eye, *if the insect is in water and is illuminated from above*.

The special point of the experiment is this: During *creeping* on a table top, in air, or on vegetation under water, the opposite legs of each locomotor pair are in alternate phase, the diagonally opposite

legs being in phase; if the two anterior (raptorial) limbs are used (as may be the case) they too work alternately, but the raptorial pair is not closely interconnected nervously with the two pairs of ambulatory legs, these last forming in reality a closely knit effector unit. But in *swimming* under water the legs of a morphological pair work synchronously, in phase; the two locomotor pairs alternate in execution of the propulsive stroke; the anterior raptorial legs, which may be

FIG. 1. Showing positions of the locomotor appendages in a swimming *Ranatra* from which both eyes have been removed. The two limbs of a pair move synchronously and in phase. At the conclusion of the stroke (dashed lines) the legs are slightly more extended than at the beginning of the stroke (full lines); as the beat of the anterior legs is concluded the posterior pair are moved to a position comparable to the initial position of the anterior limbs; thus the two pairs move in alternate phase.

used if the insect is in contact with the surface film (or, head down, with the bottom) are used alternately, though during swimming in mid-water they are inactive.

Our observations were made upon *Ranatra americana*. If both eyes of an individual are amputated, and the animal put in a large cylindrical vessel of water in a dark room, with a single point source of light above the aquarium, the *Ranatra* stays near the surface of the

water and moves aimlessly. The body remains horizontal. But if this be repeated using a *Ranatra* from which *one* eye has been removed there is witnessed a very perfect circus movement response. The positively phototropic animal swims in a compact circular path, turning continually toward the side carrying the one functional eye. If a white surface is at the bottom of the aquarium the *Ranatra* turns the eye side downward, and swims in a spiral to the bottom of the aquarium, curving always toward the remaining eye. This is continually

FIG. 2. Asymmetric tonus in legs of a swimming *Ranatra* from which one eye (right) has been removed. The legs on the blind side assume positions comparable to those of the appendages of a completely de-eyed *Ranatra* (Fig. 1). On the eye side the tonus of leg flexors is increased. This results in hydrostatic tilting of the whole body at rest. In swimming the two legs of a pair move synchronously but the greater flexor tonus on the eye side is maintained throughout the execution of the swimming stroke, so that the extension of the left legs during the propulsive motion (arrows) is less than on the relatively atonic right side. The animal accordingly swims continuously in a circle toward the eye-bearing side.

maintained for long periods. With a dead-black bottom the *Ranatra* stays at the top of the water, the eye side tilted slightly upward, and with the body almost horizontal in the surface film. Preliminary experiments have shown that the diameter of the circle in these circus movements is a function of light intensity and of wave length of light.

The important part of the observation is, that during these long continued acts of maintained orientation the two legs of each pair

work synchronously and in phase. The notion that orientation is due to a relatively greater frequency of leg movements on one side of the body is definitely disposed of. But the relative *postures* of the limbs on the two sides of the body, during movement, are quite different. The leg movements are so slow (one beat per second at 16°C.) that these facts are easily demonstrable to anyone witnessing the act of phototropic orientation, and accurate sketches can be made of the postures of the appendages. The essential facts are illustrated in the accompanying figures. Differential limb posture is therefore sufficient to account for orientation.

SUMMARY.

Definite proof is obtained that in the phototropic orientation of *Ranatra* the relative postures of the appendages, resulting in a bilateral difference of effective stroke in swimming, is the mechanism of orientation; the frequency of locomotor movements is the same on the two sides of the body.

CITATIONS.

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