

Dies lässt annehmen, dass die optomotorische Reaktion bei diesen Tieren nur eine kontrollierende Hilfsfunktion darstellt, die im Bedarfsfall durch vestibuläre Reaktionen schlagartig aktiviert wird.

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Summary

In the rabbit rotatory vestibular stimulation followed by optokinetic stimulation has a persisting facilitatory effect on the latter. The facilitation is independent of the direction of the second stimulus relative to the first one. It can therefore not be explained on the basis of the well-known addition effect in simultaneous stimulation. The neurophysiological and biological aspects of the phenomenon are discussed.

Experiments on the Sense of Time in *Talitrus saltator* (Montagu) (Crustacea-Amphipoda)

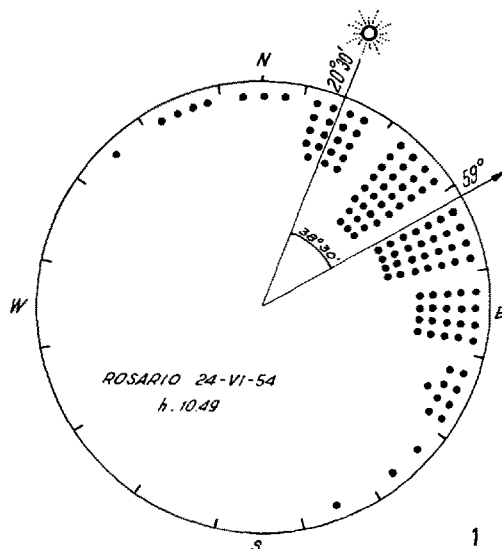
Recent researches have shown that the amphipod *Talitrus saltator* (Montagu) has a natural orientation mechanism based on the position of the sun, which permits it to maintain a determined constant direction of escape¹. The orientated escape reaction is released when animals living on the damp sand of the beach are transferred to a dry place, whereupon they attempt to return to the sea, following a line approximately at right angles to the coast. The population which was the principal object of the aforesaid research live at S. ROSSORE, near Pisa, on a coast which runs approximately in a North-South direction with the sea lying westwards. The escape direction of the individual members of this population oscillates therefore around an azimuth of 270°².

To maintain this constant escape direction, the animals assume an angle with the sun which varies during the course of the day from between approximately 180° and 0°. The orientation angles decrease from morning till sunset with the decreasing of the distance of the sun from the West. The animals in their escape almost always keep the sun on their left side, except when the sun is between East and North or between West and North.

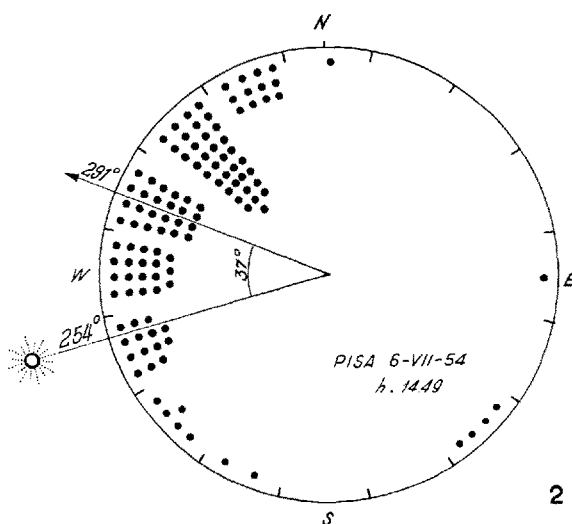
Numerous experiments have been made to discover what mechanism the animals use to modify, in a regular and continuous manner, their orientation angle with the sun during the course of the day³. Since the influence of all principal external factors on the adjustment of the orientation angle, as for example the variation of the sun's height on the horizon, were excluded, it was justifiable to conclude that the reaction depended on an interior physiological mechanism or, in other words, on a proper sense of time in the animals.

To this series of indirect proofs of the existence of a sense of time, I can now add a direct proof given by a new experiment, the logic presupposition of which is as

follows: Since the *Talitrus* makes a different angle with the sun at each hour of the day, if it were transferred to a tangibly different longitude, would it behave according to the time of the place of origin, or according to local time? In the former case, the existence of an internal time-keeping mechanism will be demonstrated, while the latter case would show that the width of the angle with the sun is adjusted according to external factors. Similar experiments have been planned long ago by FRISCH¹ for bees but not yet carried out.



Last June as N. ARRIGHINI (Pietrasanta, Lucca) had to go to Argentina he kindly offered to make the experiment. I wish to express herewith my sincere appreciation of his interest and of the accuracy with which he performed this experiment.



A group of *Talitrus* of S. Rossore (belonging to the same population of which the escape direction has been described above) was collected on the 10th of June and kept in the dark until the time of the experiment made in Rosario de Santa Fé on the following 24th of June. Thirteen *Talitrus* were put in a basin covered

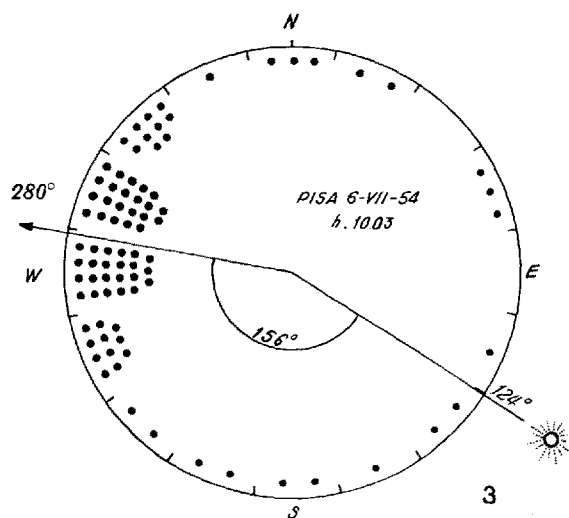
¹ L. PARDI and F. PAPI, *Naturwissenschaften* 39, 262 (1952); *Z. vgl. Physiol.* 35, 459 (1953).

² The azimuths and resulting directions are in degrees from North through East-South-West.

³ F. PAPI and L. PARDI, *Z. vgl. Physiol.* 35, 490 (1953).

¹ K. VON FRISCH, *Aus dem Leben der Bienen* (Springer-Verlag Berlin, 1941), pp. 123-124.

with a glass¹ and placed where the sight of the sky was not obstructed by objects of the landscape. The animals, as always, crowded up in determined sectors trying to escape. Their distribution was recorded by nine photographs taken between 10·38 and 11·05 h (Argentina mean solar time). Figure 1 represents the total distribution of the 117 positions observed, the resulting direction of escape, and the position of the sun at 10·49 h² (average time in which the photographs were taken). Consequently the animals on the average keep the sun on their left side by $38^{\circ} 30'$.



As soon as the results of this experiment came to my knowledge³, I performed a controlling test in Pisa with the same number of specimens at the Italian local time (14·38–15·05 h), corresponding to the time of the above-quoted experiment in Argentina. The result is shown in Figure 2. The azimuth of the sun at the average time was approximately 254° , the resulting direction amongst the 117 positions of the animals observed was 291° . Therefore the animals keep the sun on their left side by 37° . The statistical analysis of the results of this experiment and the one performed in Argentina show that the differences between the distribution in relation to the sun have no significance ($P > 0.9$). I must acknowledge that the results agree more exactly than was to be expected, considering the variability of the orientation angle even at a determined hour of the day.

Another experiment was made to establish which orientation angle the animals would assume if they had compensated for difference of longitude. Nine more photographs were taken in Pisa of a group of animals placed in a basin at approximately 10·03 h (average time), i.e. the Italian time at which the experiment was made in Argentina reduced by the difference of the time between Pisa and Rosario (approximately 4·46 h). The resulting direction between the 85 positions observed was 280° , the angle with the sun 156° (Figure 3). The difference between this distribution and the one given by the Rosario experiment appears to be statistically significant ($P < 0.001$).

¹ For the experimental methods see L. PARDI and F. PAPI 1953, l.c. (pp. 461–463).

² I wish to express my gratitude to Com. ENRICO LAJ of the Accademia Navale di Leghorn for assistance with the astronomical calculation.

³ N. ARRIGHINI, in lit. June 26, 1954.

The animals behaved therefore at 10·49 h in Rosario in the same manner as they would have behaved in Pisa at 14·49 h. Consequently it is proved that the *Talitrus*, transferred to a different longitude, adjust their orientation angle with the sun according to the time of the place of origin and not according to local time. This phenomenon demonstrates the existence of an internal sense of time¹.

F. PAPI

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Riassunto

Il Crostaceo Anfipode *Talitrus saltator* (Montagu) possiede un meccanismo di orientamento solare che gli permette, mediante una variazione regolare e continua dell'angolo di orientamento nel corso del giorno, di mantenere una direzione di fuga praticamente costante. Esemplari del litorale tirrenico, trasportati in Argentina, hanno assunto un angolo di orientamento col sole conforme all'ora italiana nel momento della esperienza. Ciò dimostra che la regolazione dell'angolo di orientamento è dovuta ad un fattore endogeno e cioè che esiste in *Talitrus* un senso del tempo.

¹ L. PARDI and M. GRASSI (cfr. this same number) comes to the same conclusion, following different method.

Experimental Modification of Direction-Finding in *Talitrus saltator* (Montagu) and *Talorchestia deshayesi* (Aud.) (Crustacea-Amphipoda).

By influencing the time-keeping mechanism ("innere Uhr") of starlings, K. HOFFMANN¹ succeeded in modifying a given direction-finding that these birds had learnt in connection with the position of the sun.

After training two starlings to find food in a given direction, HOFFMANN placed the birds in a dark room and subjected them to an illumination 6 h behind-hand in respect to normal conditions, i.e. the animals were kept in artificial light from 6 h after local sunrise to 6 h after local sunset. The temperature also was adjusted to conform with the new light conditions. After 12–18 days of this treatment, their steering by the sun for the direction they had learnt was modified exactly as expected. For example, the bird trained to find food to the west now sought it towards north, which can easily be accounted for, on recollecting that the "internal watch" of the animal was 6 h late. HOFFMANN, moreover, proved that when the animals are again subjected to normal conditions of light (in the open air), they return to the direction learnt in their early training within a period of not more than 12 days.

It was interesting to apply this beautiful experiment of HOFFMANN to *Talitrus*, for this Amphipod can steer its course on the shore in reference to the azimuthal position of the sun (mirror experiment) (PARDI and PAPI; AURICH in VON BUDDENBROCK; PAPI and PARDI²).

Specimens removed from the moist sand return to it at any time of day, always following a more or less

¹ K. HOFFMANN, *Naturwissenschaften* 40, 608 (1953).

² L. PARDI and F. PAPI, *Naturwissenschaften* 39, 162 (1952); Z. vgl. Physiol. 35, 459 (1953). – AURICH in W. VON BUDDENBROCK, *Sinnesphysiologie*, Verlag Birkhäuser (1952). – F. PAPI and L. PARDI, Z. vgl. Physiol. 35, 490 (1953).