

Anemomenotactic Orientation in Beetles and Scorpions¹

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SCORPIONS, living in North African semi-deserts are—in spite of disrupting experimental interferences—able to maintain a certain direction in their natural environment in the dark on a plane surface. Under comparable laboratory conditions, excluding the possibility of light or gravity orientation, they can orient themselves if a directed air current passes over the “arena.”

In most cases the scorpions do not run necessarily with or against the wind, but rather maintain constant angles to the air current for anywhere from minutes to many hours. They are running anemomenotactically (ref. 1). Under identical conditions many species of beetles also orient themselves to air currents (refs. 2 to 4). The main problems to be solved in the study of anemomenotactic orientation are:

- (1) Which physical qualities of the air current have an influence on the anemomenotaxis?
- (2) With which sense organs do beetles and scorpions perceive wind directions?
- (3) Which physiological mechanism is the basis of anemomenotactic orientation?
- (4) What is the biological significance of anemomenotaxis in beetles and scorpions?

With respect to these problems, more study has been done on beetles than on scorpions. Therefore, due to lack of space, I shall discuss mainly some of the results obtained in experiments with dung beetles (*Geotrupes silvaticus*, *G. stercorarius*, *G. armifrons*, *G. niger*, *Scarabaeus variolosus*) and tenebrionid beetles (*Tenebrio molitor*, *Pimelia grossa*, *P. tenuicornis*, *Scaurus dubius*).

METHODS²

The horizontal arena (diameter 1 m) was placed in an octagon that screened out daylight and ambient air currents. The directed horizontal wind is produced by adjustable ventilators (with a rotating drum fan). After every run to the brink of the arena the beetles are returned to the center of the running area. The direction of the wind stream in each experiment was repeatedly changed.

At first only pure anemomenotaxis was to be investigated, and every possibility of incident-light orientation had to be excluded.

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² For more details see Linsenmair (refs. 3 and 4).

The beetles, reacting to red light with a wavelength of over 6100 Å (Osram 5463), were blinded by an opaque laquer. In dung beetles it was sufficient to cover the upper half of the divided eyes in order to exclude directing effects of the red light. Experiments with scorpions, with all eyes laquered, had always to be performed under red light because only then light reactions not mediated by the eyes could be avoided.

RESULTS

Physical Qualities of the Air Stream

The lowest wind velocity which would evoke menotactic orientation in dung beetles was about 0.15 m/sec; it was about 0.4 m/sec in *Pimelia* and about 0.5 m/sec in *Tenebrio*. The limiting velocities against which the beetle can not move are 2.5 to 4.5 m/sec, depending on size of the beetle and the nature of the surface on which it is running; this upper limit also applies to scorpions. In the lower range however scorpions react anemomenotactically to air currents with speeds of only 0.02 to 0.05 m/sec. For scorpions and beetles, changing of wind velocities—within the mentioned limits—has no effect on the anemomenotactic angle (refs. 1 and 3).

Beetles can orient themselves in discontinuous horizontal winds, if the wind puffs are not too short and the intervals of still air are not too long. Experiments with dung beetles and scorpions on an extremely rough surface that caused strong air turbulences show that orientation is not greatly affected by such disturbances (ref. 3).

Wind Perception

Weeks after an amputation of both antennae a beetle does not orient to air currents. However, it was found that as few as

two segments of the flagellum on each antenna are sufficient to allow a dung beetle to orient anemomenotactically if the wind velocity is at least 1 m/sec. Fixing joints of the antenna by laquer shows that only the flexibility of the pedicellus-flagellum joint is necessary for anemomenotaxis. Movements in this joint—as we know from many insects—are perceived mainly by the Johnston-organ (refs. 5 to 8). It therefore seems obvious that also in the running beetle the Johnston-organ perceives air currents and detects their direction. In scorpions the trichobothria fulfill these tasks.

Physiological Mechanism

There are two theories to explain the special performances of menotaxis:

(1) Janders (refs. 9 and 10) "compensation theory"

(2) Mittelstaedts (refs. 11 and 12) theory of the "reciprocal modulation of bicomponents"

Because Janders' theory is less complicated, we shall see first whether or not this theory can explain the experimental findings.

The functional organization of menotaxis is explained by the compensation theory in the following way. The bases for menotaxis are the two basic orientations, the positive and the negative taxis. For example, in the positive basic orientation a deviation from the positive basic direction (i.e., a deviation from the position exactly against the stimulus direction) causes a reactive turning excitation. This "afferent turning tendency" leads, over the smaller angle, back to the positive basic direction and is in strength dependent on the amount of deviation. In switching over from the positive to the negative basic orientation the turning directions of this turning tendency are reversed, thus inducing the animal to turn to the negative basic

direction via the shortest path. Basic orientations are assumed to participate in menotaxis, determining patterns of turning tendency directions and turning tendency strengths as in basic orientations. All menotactic runs not deviating more than 90° from the positive stimulus direction are supposed to be based on positive basic orientation (the turning tendency therefore always leading to the positive basic direction), whereas those aiming in the opposite directions ($\pm 90^\circ$ to 180°) are supposed to be based on negative basic orientation. Because the turning tendency always would force the animal to turn back to the basic direction of the "switched on" basic orientation, the compensation theory postulates the existence of a second, opposite directed and centrally generated, turning excitation—the "efferent course order." If the menotactic set angle is reached, the two equally sized turning excitations, opposite in their directions, are assumed to neutralize each other.

One should be able to disturb this equilibrium by, for example, suspending the turning tendency (by the sudden removal of the directing stimulus). In figure 1, results of such experiments are summarized. In the anterior half of the circle (quadrants I and IV) the beetles—in a highly significant percentage—turn away from the direction of the wind stream; in the posterior half (quadrants II, III) however they choose the opposite turning direction, with respect to the wind direction. The angle size within a quadrant does not influence the direction of the turning. These results are in accord with the compensation theory; not only the course order becomes apparent as a directed turning excitation, but the demonstration of opposite turnings in adjacent quadrants makes the participation of both basic orientations in anemomenotaxis very probable. In the anterior half of the circle the beetles turn away from the

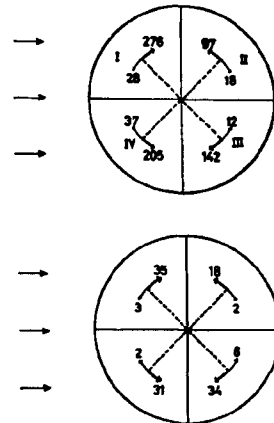


FIGURE 1. Directions of turning movements induced in anemomenotactically oriented *Geotrupes* (1a) and *Pimelia* (1b) by a sudden interruption (see Linsenmair ref. 3) of the air current. Arrows pointing toward the circle in all graphs symbolize wind direction.

positive basic direction, while in the posterior half they turn away from the negative basic direction. This distribution of turning directions, after a suspending of the turning tendency, has to be expected if the basic orientations are, as postulated by the compensation theory, responsible for the directions of the turning tendency, and if, with respect to the corresponding set angle, the turning tendency always is compensated by an opposite-directed course order.

In figure 2, the distribution of the running directions of four dung beetles is presented. Their individual preference direction lay between 27° and 32° right of the positive basic direction. The runs not aiming in the preference direction are not evenly distributed over the rest of the circle, but are concentrated in an adjacent quadrant. If one compares the mean angle deviation of the runs from the next basic direction in the two quadrants most often chosen, then the following null hypothesis proves correct: With re-

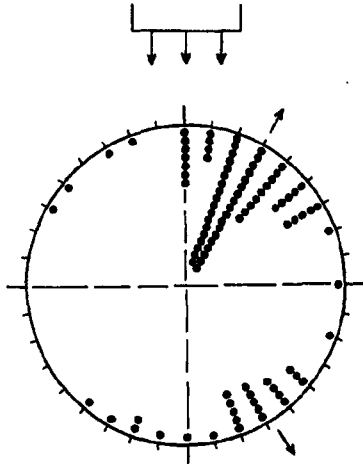


FIGURE 2. Distribution of the anemomenotactic courses of four dung beetles, all of which maintained a preference direction of about 30° to the right of the positive basic direction. The two arrows pointing away from the circle show the preferred angle sizes within the two quadrants most often chosen. Every point represents two runs.

spect to the basic directions all four dung beetles in both quadrants kept the same preference-angle size with the same standard deviation. While the choice of the quadrant may be strongly influenced, the mean deviation from the basic directions in the intact beetle normally remains constant under different conditions as well (see ref. 3). When one correlates two succeeding runs of dung or tenebrionid beetles in different quadrants, one gets the results shown in figure 3. A correlation analysis proves that a beetle running successively in two of the four quadrants generally maintains his angle size. This "intramodal transposition" (ref. 13) is easily understood in assuming that:

- (1) Course orders cannot lead to deviations from a basic direction exceeding 90°
- (2) That the turning direction of the course order and/or the turning direction of

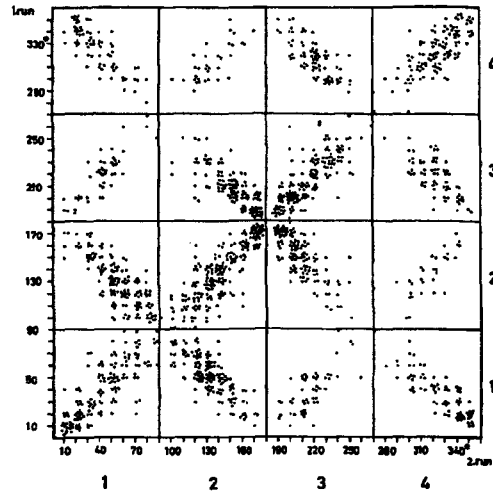


FIGURE 3. Correlation diagram: Evidence of the fourfold intramodal angle size transposition in *Geotrupes*. All correlation modi are highly significant ($p < 0.005$).

the turning tendency may be reversed, without changing the strength of the course order (ref. 3)

These findings are also not contradictory to the compensation theory.

By another method, information about the physiological mechanism of anemomenotaxis has been gained which confirms the mentioned findings.

Under natural conditions air currents normally effect both antennae. Here the question arises about the kind of interaction between the specific sense organs of the pair of antennae. Figure 4 shows a typical result. After amputation of one antenna (or after blocking the pedicellus-flagellum joint by laquer) the mean size of the running angle increases. In the case that the size of the course order is not affected by the exclusion of one antenna, the elimination causes a decrease in the strength of the turning tendency. This supports the hypothesis of a synergistic interaction of the paired antennal

organs and opposes the main alternative hypothesis of an antagonistic—i.e., tropotactic—interaction. The fact that it is of no influence on the menotactic angle size whether the left or the right antenna is amputated supports also the idea that the excitations of the paired sense organs are summed up.

Figure 4 shows that the elimination of one antenna leads to an approximate doubling of the angle size. This result suggests that the antennae are equivalent synergists. If this assertion is valid without limitations, then there should be a range of running angles, in which the halved turning tendency of the amputated beetle cannot compensate the unchanged course order. In these cases the beetle should rotate. This expectation is proved only partly by results presented in figure 5. Indeed some beetles rotate which had, when intact, kept angles of about 30° or more. But in this range of angle sizes, after an elimination of one antenna, one finds not only very different augmentations of the running angle, starting from the same "intact-

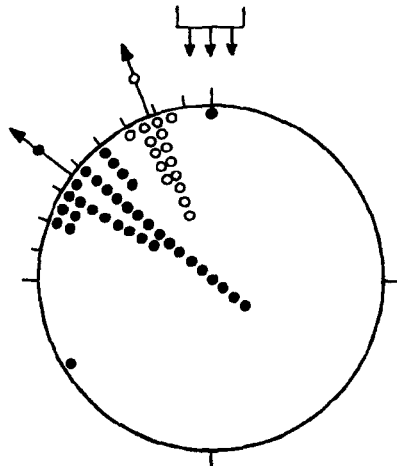


FIGURE 4. Distribution of the running courses of a dung beetle before (circles) and after (points) complete amputation of its right antenna.

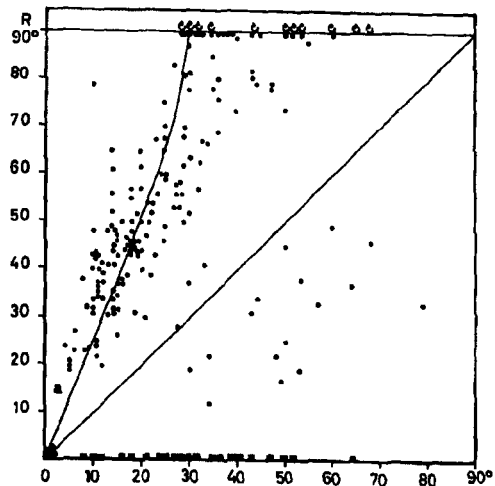


FIGURE 5. Mean angle sizes of the run series of dung beetles ($n = 139$ beetles, about 11 000 single runs) with one antenna excluded (ordinate) independent of the angle size maintained before the exclusion (abscissa). Bent arrows within the R-line symbolize rotations of the beetles. Some beetles, after an exclusion of one antenna, change over from the anemomenotactic to a basic (anemotactic) orientation (squares on the 0° line; see Linsenmair ref. 4). The curve *a* is to be expected if there is a sine function between the stimulus direction and the strength of the turning tendency, and if the exclusion of one antenna is always followed by a 50 percent reduction of the turning tendency strength. Because of the four-fold intramodal transposition, and other experimental evidence, it is justified to treat the size of a menotactic angle (measured as the amount of angle deviation from the next basic direction) without taking into account its direction (within the range of 360°).

angle," but also significant reduction of angle sizes.

Beetles running first with intact antennae, then with one antenna eliminated by reversible laquering, and finally again with both antennae intact show the reactions presented in figure 6. If the running angles maintained in the "preliminary experiment" are not big-

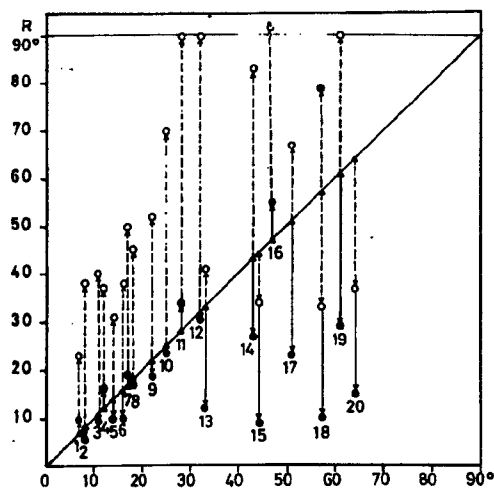


FIGURE 6. Changes in the mean angle sizes after a reversible exclusion of one antenna (ordinate). Triangles are mean angle sizes in the "preliminary experiment" (abscissa). Dashed arrows with circles are directions and amount of changes in angular size in the "main experiment". Solid arrows with points are changes of angular size in the "control experiment" in comparison with the angle size in the preliminary experiment. (Dashed dotted arrow in beetle 18: sudden spontaneous change of angular size, from about 10° to about 80°, in the control experiment.)

ger than about 30° then the angle sizes are augmented significantly in the second experiment, the "main experiment." In the third experiment, the "control experiment," the again intact beetles resume the same or nearly the same angles as in the preliminary experiment. The augmentation of the running angle sizes in the main experiment therefore has to be attributed only to a reduction of the strength of the afferent turning tendency.

Angles bigger than 30° in the preliminary experiment may be augmented or diminished. The amount and the mode (i.e., increase or decrease) of the change in angle size cannot

be predicted. What can be predicted, however, in these beetles is amount and mode of change in angular size from the main to the control experiment: The angular size always is approximately halved (see fig. 6). The menotactic angles then maintained by these beetles in the control experiment are regularly smaller than in the preliminary experiment. This fact obviously demonstrates that the strengths of course orders, leading to running angles in excess of 30° in the preliminary experiment, are in all beetles diminished, which can still keep a straight course in the main experiment.

Preference angles of about 90°, after elimination of one antenna, are based on course order strengths leading in the intact beetle (in the control experiment) to angular sizes of about 30°. Angles larger than 30° cause rotations in the main experiment (see fig. 6, beetle No. 16) if the course order strength is not reduced. These findings together with the varying scale of angle enlargements in the range from 0° to 30° (see fig. 5) make a sinusoidal relationship between stimulus direction and strength of turning tendency very probable.

Elimination of one antenna is not followed by a loss of the essential qualitative performances of the anemomenotaxis. Beetles with only one intact antenna can determine the wind direction. They can steer anemomenotactically unambiguous directions relative to the air current and are—after a forced deviation—able to turn back to their preferred direction over the smaller angle. Quantitatively—in evaluating the stimulus direction by a certain strength of the turning tendency—one antenna shows only half the capacity. As would be expected, if there is an equilibrium between two antagonistic forces, the course order has a doubled efficiency after the turning tendency is halved. The running angle is doubled (see previous discussion of

intact angles larger than 30°). Likewise, the course order efficiency is always halved if, after a reversible elimination of one antenna, the beetle runs again with both antennae intact. Especially important is the evidence that the menotactic angle size, after enlargement caused by an elimination of one antenna, never exceeds 90° , as measured from that basic direction to which the turning tendency leads and from which the course order deviates. If a course order leading to a running angle larger than 30° is not diminished after elimination of one antenna, the beetle does not run into the adjacent quadrant, but rotates. In a beetle running into an adjacent quadrant after one of its antennae was eliminated, it can always be demonstrated that it transposes angles (ref. 4).

Mittelstaedt (refs. 11 and 12) makes two objections, one depending on the other, against the compensation theory:

(1) The theory offers no explanation of how an animal can steer a menotactic course beyond 90° .

(2) The theory does not explain the equally sized and equally directed shift of the stability and the lability positions.

A purely additive superposition of a course order, with the sign remaining constant, over the sinoidal turning tendency must lead to an approximation of the positions in which both opposite turning exciting excitations are in a labile equilibrium—position—and the position in which the turnings are in a constant equilibrium—stability. They coincide with each other at $\pm 90^\circ$, lability position (refs. 11 and 12, 14 and 15). Therefore courses deviating by 90° from a basic direction should be very unstable, and angles beyond 90° could not be steered by such a mechanism. Numerous experimental results show, that in the anemomenotaxis of the investigated beetles a course order of the maximum amount can not deflect the beetle

to a deviation exceeding 90° from a basic direction. But still there would be the instability of 90° courses, if the course order was superimposed by addition (demonstrated by Schöne (ref. 14) in the photomenotaxis of dydiscid larvae). Above all, beetles not always were able to turn back to their preference direction over the smaller angle. Deviations from this principle of "the shortest turning way" are not found in a group of beetles orienting anemomenotactically. Also some beetles, when one antenna is eliminated, turn promptly, and some turn much later over the smaller angle back to their preference direction. Stability and lability positions thus lie opposite to each other in anemotaxis as well as in anemomenotaxis. How does this finding fit in a compensation mechanism?

The turning tendencies in the right and the left half of the circle have different signs, if the beetle runs in a basic direction; in deviating into one half it turns to the right, in the other half, to the left. The opposite signs do not disturb the anemomenotactic orientation mechanism, because a beetle cannot run at the same time in both halves of the circle. In supposing that also the signs of the course order are always reverse in the anterior and posterior half of the circle, all previous results concerning the anemomenotaxis of beetles are consistent with a compensation mechanism (figs. 7 and 8; compare to ref. 16).

Biological Significance of Anemomenotaxis

Whenever possible scorpions orient relative to landmarks. Sometimes light sources (e.g., the Sun or Moon) give the essential directing stimuli. As soon as one eliminates visual orientation possibilities, it turns out that scorpions permanently take notice of the direction of the wind. Where vision served before, the scorpions learn to keep their

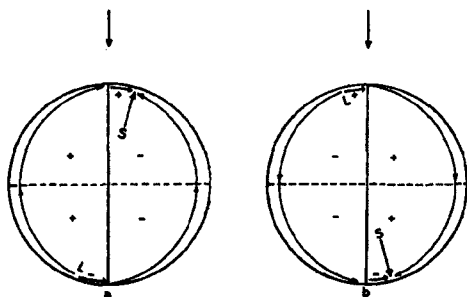


FIGURE 7. Turning movements (directions of arrows) observed after deviations from the stability position *S* in anemomenotactic oriented beetles. In *L*—the liability position—turns to the right and to the left are equally frequent, in all other cases the beetles take the shorter way. Thick arrows show the ranges in which observed turning movements are opposite to those of a positive (7a) or negative (7b) anemotactic beetle. It is proposed that these turns are induced by the course order, which is assumed to act in the anterior and posterior half of the circle with reversed signs of the turning direction. Between 7a and 7b an angle transposition took place, in which not only the taxis was switched over (the signs of the direction of the turning tendency are reversed in the right and the left half of the circle) but also the sign of the course order direction. (Movements to the right are "+", to the left "-".)

course by pure anemomenotaxis (or anemotaxis). As far as is known scorpions possess no sense of smell. Probably the main task of anemomenotaxis is to provide a sense of space orientation which, like in many cases photo- or geomenotaxis, allows the animal to keep a straight course. Because the scorpions are nocturnal, and because in their natural environment there is a nearly continuous wind varying only occasionally in direction, the anemomenotaxis is of great value.

In the lives of the investigated beetles, stimuli perceived by osmoreceptors are of great importance. While at very short range a pure osmotropotactic or osmoclinotactic orientation may lead to the source of a smell

(refs. 17, 18 and 19), one can hardly imagine how such a mechanism could work in an osmic orientation over long distances. Several authors (refs. 20 to 23) suggest that long distance olfactory orientation is not possible without positive anemotaxis.

Also those animals in which an osmic sign stimulus releases a positive anemotaxis are forced to search the sign stimulus. Here one should look for the main task of the beetles anemomenotaxis. This supposition is supported by observations of different species of dung beetles in their natural habitat; in search for food, running dung beetles choose a menotactic course to the wind direction. Thus they can "oversmell" a maximum area in a minimum of time.

If the beetle's attention is drawn to the smell of dung while flying he often lands more or less far from the dung; as this beetle, also a scarabaeus—having lost his dung ball on a slope—knows in which approximate area it has to search. In such cases one does not only recognize the biological significance of anemomenotaxis but also that of the ability to transpose anemomenotactic angle sizes intramodally. The beetles, maintaining at first an angle of say 30° to the right of the positive basic direction, after a run of some length make a turn of 60° , maintaining then a course of 30° to the left from the positive basic direction. The result is a zigzag course, which is especially appropriate in tracking a smell source of which the approximate position is known.

Thus the anemomenotaxis is a very important part in the appetitive behavior of dung beetles "waiting" for an olfactory sign stimulus. As soon as the dung beetle has found that sign stimulus it changes its direction and runs against the wind. The question how this positive anemotaxis and the osmic orientation interact has to be answered by further experimental investigations.

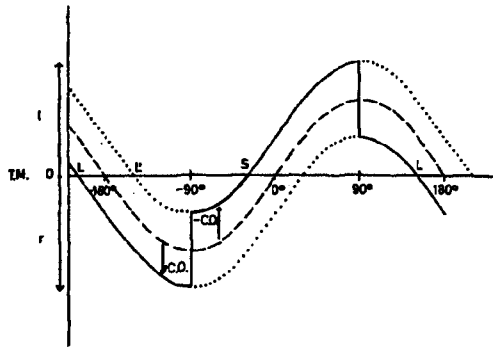


FIGURE 8. In a pure additive superposition of course order (C.O.) over sinusoidal anemotactic turning tendency (dashed sine curve, set angle 0°) stability and liability positions are, in increasing angle sizes, approaching each other; for example, S and L' in the upper, partly dotted, partly solid, sine curve. They coincide in $\pm 90^\circ$. [A course order showing a turning direction to the right is called positive (+ C.O.), a course order with a turning direction to the left negative (— C.O.).] In the case of the upper and lower sine curve, an animal, deviating into the range from -150° over 180° to $+150^\circ$, could not turn back to its set direction (-30°) over the smaller angle [r equals turning movements (T.M.) to the right, l equals turning movements to the left]. In assuming reversed signs of the course order in the anterior and posterior half of the circle, one attains the solid curve: Stability position S and liability position L now lie opposite to each other. In deviating from its set course, the animal always can turn back over the shorter way.

SUMMARY

1. Scorpions and beetles can orient menotactically to the direction of horizontal air currents. Changing the wind velocity, within the range releasing anemomenotactic orientation, does not influence the size of the menotactic angle. The anemomenotactic orientation is not seriously affected by discontinuities and turbulences of the air current.

2. In scorpions the trichobothria perceive

the direction of the wind. In the investigated beetles air current directions are perceived by sense organs excited by movements in the pedicellus-flagellum joint.

3. The experimental findings suggest a compensation mechanism as the basis for anemomenotactic orientation in beetles. A straight menotactic course can then be maintained when the "afferent turning tendency" is compensated by an opposite directed "efferent course order" of equal size. Both basic orientations, positive and negative anemotaxis, participate in the anemomenotaxis and determine the pattern of turning directions and turning strengths of the turning tendency. The function between the strength of the turning tendency and the stimulus direction is sinusoidal. As to be expected in a compensation mechanism the maximum size of a menotactic angle is 90° . By maintaining the strength of a course order and by reversing their turning direction and/or the turning direction of the turning tendency the beetles can transpose menotactic angle sizes. Also the fact, that in anemomenotaxis the stability and the liability position lie opposite each other is consistent with a compensation mechanism; we only have to assume that the turning direction of the turning tendency in the right and the left half of the circle, and the turning direction of the course order in the anterior and posterior half of the circle are always reverse.

4. The interaction of the paired antennal sense organs of the beetles perceiving wind directions is synergistic. The exclusion of one antenna is followed by a 50% reduction of the strength of the turning tendency.

5. The main biological significance of anemomenotaxis in scorpions is suggested in space orientation. Whereas in beetles it is evident, that the anemomenotaxis is an important part of the appetitive behavior of beetles "searching" for olfactory sign stimuli.

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