How animals use their environment: a new look at kinesis

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Abstract. The aim of this paper is to show how animals can orient themselves in relation to a stimulation gradient or exploit patchy environments using simple kinetic mechanisms. From a new look at klinokinesis and orthokinesis, the properties of these two mechanisms were determined and their respective contributions to the phenomenon of animal aggregation in the most suitable areas of the environment were specified. When movement regulation is a function of variations in the stimulus intensity, klinokinesis can be seen as an elementary spatial orientation mechanism, whereas orthokinesis seems to have no biological application. In contrast, when movement regulation is a function of the value of stimulus intensity, klinokinesis and orthokinesis can both be seen as elementary space-use mechanisms. Some examples of applications of the models are given. In particular, it is suggested how klinokinetic and orthokinetic models can formalize the 'area-restricted' searching behaviour exhibited by many foraging animals. Finally, the place of klinokinetic and orthokinetic mechanisms in the framework of a general theory of spatial orientation and space use in animals is discussed.

The ways in which animals use their environment can be explained, under some conditions, in terms of simple kinetic mechanisms. For this purpose it is necessary, on the one hand, to distinguish what relates to spatial orientation from what relates to space use (sensu stricto), and, on the other hand, to identify those environmental cues that are relevant for animals and those kinetic parameters of their movements that they have to control to be efficient. Previous studies based on klinokinesis and orthokinesis have been misleading because they failed to fulfill properly these preliminary requirements (see below). Taking a new look at these two types of kinesis, we attempt in this paper to elucidate some of the mechanisms used by animals to orient themselves in relation to a stimulation gradient or to exploit patchy environments.

Klinokinesis and orthokinesis were defined by Gunn et al. (1937), and thereafter by Fraenkel & Gunn (1940, revised 1961), to explain animal aggregation in the most suitable areas of the environment in terms of simple mechanisms. According to these definitions, klinokinesis and orthokinesis correspond to elementary locomotor reactions, consisting of a regulation of the rate of change of direction (or angular velocity), and of the (linear) velocity, respectively, of a random movement in response to local environmental conditions. In addition, two functional modes were distinguished. In the first mode, classically called 'without (sensory) adaptation', the regulation is a function of the actual value of the stimulus intensity. In the second mode, classically called 'with (sensory) adaptation', the regulation is a function of variations in stimulation intensity which are perceived during the movement. We shall refer to the first and second modes as the absolute and differential mechanisms, respectively. Some historical examples of klinokinesis and orthokinesis were given by Fraenkel & Gunn (1961). More recent examples have dealt with the movements of bacteria (Berg & Brown 1972; MacNab & Koshland 1972, 1973; Tsang et al. 1973; Van Houten 1978), planarians (Stasko & Sullivan 1971; Mason 1975) and beetles (Havukkala 1979, 1980; Havukkala & Kennedy 1984).

The original definitions of klinokinesis and orthokinesis are still being used in movement models (see Van Houten & Van Houten 1982; DeAngelis & Yeh 1984). They have nevertheless led to great confusion about the properties of these mechanisms, because they were both based on spatio-temporal concepts, the rate of change of direction and the velocity, respectively, in order to account for the same phenomenon of animal aggregation. The rate of change of direction of a given path varies with the velocity, so that the joint use of these concepts makes it impossible to distinguish between the respective roles of the spatial and temporal components of the movement.
in question. As Gunn (1975) has mentioned, application of klinokinetic and orthokinetic models to metazoans is possible only if the different mechanisms involved can be clearly distinguished.

In line with previous studies (Bovet 1984; Bovet & Benhamou 1985; Bovet et al. 1986), we propose a redefinition of klinokinesis which consists of replacing the old spatio-temporal concept of rate of change of direction with the purely spatial concept of 'sinuosity' (expressing the amount of turning associated with a given path length). To formalize the sinuosity concept, let us consider any search path to be a first-order correlated random walk. It is represented in the form of a sequence of \( N \) steps with length \( P \), and the changes of direction between them are randomly drawn in a normal distribution with a null mean and a standard deviation \( \sigma \). Dividing paths into discrete steps is a useful way of representing them, but steps do not often correspond to any biological parameter. To quantify the chaotic path structure by a single numerical index which is independent of the arbitrary choice of the step length, we calculated sinuosity as the ratio between the standard deviation of the distribution of changes of direction and the square root of the step length \( S = \sigma / \sqrt{P} \) (expressed in rad/\( u \)^{1/2}, where \( u \) is the unit of step length; Bovet & Benhamou 1988).

We propose, however, to keep the original definition of orthokinesis. Klinokinesis and orthokinesis are then defined as probabilistic models which formalize mechanisms regulating the sinuosity and the velocity of movement, respectively, on the basis of either the local value of the stimulation intensity (absolute mode) or its variations (differential mode). We then attempt to determine the properties of these two mechanisms and to specify their respective contributions, in the differential as well as the absolute mode, to the phenomenon of animal aggregation in the most suitable areas of the environment.

**DIFFERENTIAL KLINOKINESIS**

Let us consider an animal that moves in what we refer to as a 'stimulation gradient field', i.e. an environment containing a monotonously varying stimulus. The stimulation intensity depends on the position of the animal in space, so that the ratio between the variation in intensity perceived by the animal during a step (\( dI \)) and the step length (\( P \)) provides it with relevant information about the orientation of this step in relation to the gradient direction. For the sake of simplicity, the stimulation intensity is assumed to increase linearly along the gradient axis. The intensity variation \( dI \) is then given by

\[
dI = aP \cos \theta, \quad \text{with} \quad a > 0
\]

where \( \theta \) is the orientation of the step with length \( P \) that the animal just walked in relation to the gradient direction, and \( a \) is the slope of the intensity function. Again for simplicity, the differential klinokinetic mechanism is assumed to regulate the sinuosity as a linear function of \( dI/P \)

\[
S = S_b(1 - b \frac{dI}{P}) = S_b(1 - k \cos \theta), \quad \text{with} \quad k = ab
\]

We refer to \( S_b \) as the basic sinuosity and to \( k \) as the klinokinetic factor. The value of \( S_b \) corresponds to the sinuosity with which the animal moves when there is no stimulation gradient (\( k = 0 \)). That of \( k \) (ranging between \(-1 \) and \(+1 \)) expresses the normalized intensity of the regulation of the sinuosity. It depends on both the gradient intensity (given by \( a \)) and the sensitivity of the animal towards the stimulus (given by \( b \)).

Using computer simulations, we observed that the differential klinokinetic mechanism leads to a drift of animals in the direction of the gradient (Fig. 1). It is therefore responsible for a tendency for animals to aggregate in the most suitable region of the environment, where the intensity of stimulation will be either strong or weak, depending on whether the stimulus is attractive (\( k > 0 \)) or repulsive (\( k < 0 \)). The klinokinetic drift indicates that a differential sinuosity regulation mechanism allows animals to orient their movements in a stimulation gradient field, without any perception of the stimulation source. The differential klinokinetic model thus formalizes an elementary sensori-motor directional mechanism (Bovet & Benhamou 1985): it considers animals to be probabilistic self-directed mobile agents.

It is important to note that regulation of the sinuosity \( S = \sigma / \sqrt{P} \) can be performed by varying the standard deviation of the distribution of changes of direction \( \sigma \) (first case) as well as by varying the step length \( P \) (second case). As underlined above, dividing paths into discrete steps is often only a useful way of representing them. Consequently, it must be kept in mind that klinokinesis actually involves a regulation of sinuosity, whatever the technical means (first or second case) used to formalize it.

In the first case, keeping a constant step length \( P \),
Figure 1. Klinokinetic drift of 100 theoretical animals, from the point of origin 0, after a path comprising 1000 steps with a constant length $P$, within a stimulation gradient field (parallel to the $X$-axis), as obtained by computer simulation. In this example, the sinuosity regulation occurring after each step is given by $S = 0.5 (1 - 0.5 \cos \theta)$, where $\theta$ is the orientation of the step in relation to the gradient direction. Only five paths have been completely drawn. The last point of each of the 100 paths is represented by a cross.

Figure 2. Efficiency of the differential klinokinetic mechanism $E(D_k/L)$ as a function of the klinokinetic factor $k$ and the basic sinuosity $S_b$ ($\sigma_b$ arithmetically ranging between 0.2 and 1.0 rad). Each of the 51 points was obtained from 500 simulated paths comprising 1000 steps with a constant length $P$ (path length $L = 1000P$). $E(D_k/L)$ is proportional to $k$ and nearly independent of $S_b$. (For each value of $k$, the different crosses represent the values of $E(D_k)$ obtained with the different values of $S_b$.) The dotted line represents the function $E(D_k/L) = 0.95k$.

The differential klinokinetic mechanism is expressed by $\sigma_i = \sigma_{b_k}(1 - k \cos \theta_i)$ where $\theta_i$ is the orientation of the $i$th step in relation to the gradient direction. The orientation of the first step is drawn in a uniform distribution and the values of changes of direction ($\alpha_i = \theta_{i+1} - \theta_i$) are drawn, independently from each other, in a normal distribution $N(0, \sigma)$. The basic sinuosity is given by $S_b = \sigma_b/\sqrt{L}$. It can easily be demonstrated that the expected value $E(D_k)$ of the klinokinetic drift $(D_k)$ of an animal, as measured by its position along the gradient axis, is proportional to the path length ($L = NP$)

$$E(D_k) = NE(P \cos \theta) = LE(\cos \theta)$$

We quantified the klinokinetic drift as a function of $\sigma_b$ and $k$ using computer simulations. Nine values of $\sigma_b$, arithmetically ranging between 0.2 and 1.0 rad, and eight values of $k$, arithmetically ranging between 0.1 and 0.8, were chosen such that $\sigma$, which varies within the interval $[\sigma_b(1-k), \sigma_b(1+k)]$ was always restricted to between 0.1 and 1.2 rad (see Bovet & Benhamou 1988). With each value of $\sigma_b$ and with each value of $k$ (51 possible combinations), 500 paths comprising 1000 steps (path length $L = 1000P$) were simulated. As shown in
Fig. 2, the efficiency of this differential klinokinetic mechanism, measured by $E(D_k/L)$, is proportional to the klinokinetic factor $k$ and nearly independent of the basic standard deviation $\sigma_b$, and therefore of the basic sinuosity $S_b$. By the least squares method, the proportionality coefficient expressing $E(D_k/L)$ as a function of $k$ was estimated to be 0.95.

In the second case, keeping a constant value of $\sigma$, the differential klinokinetic mechanism is expressed by $P_i = P_b/(1 - k \cos \theta)^2$. The orientation of the first step is drawn in a uniform distribution and the values of changes of direction are randomly drawn in a normal distribution $N(0, \sigma)$. The basic sinuosity is given by $S_b = \sigma/\sqrt{P_b}$. Following this process, 500 paths comprising 1000 steps were simulated for 12 values of $\sigma$ arithmetically ranging between 0.1 and 1.2 rad, and for nine values of $k$ arithmetically ranging between 0.1 and 0.9 (108 combinations). The results were nearly the same as those obtained in the first case. The expected drift $E(D_k)$ is proportional to the path length $L$ and to the klinokinetic factor $k$, and fully independent of the basic sinuosity $S_b$: the proportionality coefficient, as estimated by the least squares method was 1, however, with any value of $S_b$.

Furthermore, although the concept of sinuosity is formally based on a first-order correlated random walk model, a particular form of differential klinokinesis involving a regulation of the step length can be defined from the simple (non-correlated) random walk model, where changes of direction are drawn in a uniform distribution. In this way, 500 paths comprising 1000 steps were simulated with the nine values of $k$ arithmetically ranging between 0.1 and 0.9, and the proportionality coefficient was still estimated by the least squares method to be 1.

It can therefore be said that the mean drift generated by this differential klinokinetic mechanism, whether it consists of regulating the standard deviation of the distribution of changes of direction or of regulating the step length, regardless of the distribution of changes of direction, is very close to the product of the path length and the klinokinetic factor

$$E(D_k) \approx kL$$

This drift is thus a purely spatial property. It is possible, however, to express it in a dynamic way as a function of time, by taking the product of the mean velocity and the time of travel instead of the path length. The mean klinokinetic drift per unit of time is equal to the product of the klinokinetic factor and the mean velocity.

**ORTHOKINESIS**

From the original definitions by Gunn et al. (1937) and Fraenkel & Gunn (1940), Rohlf & Davenport (1969) have shown, using computer simulations, that the differential klinokinetic and orthokinetic mechanisms are both able to lead to an aggregation of animals in the most suitable region of a stimulation gradient field. This result is not surprising, since the two mechanisms formalized by these authors on the basis of the rate of change of direction and the velocity both involve variations in the sinuosity of the path as a function of the variations in the stimulation intensity perceived during the movement, by varying either the standard deviation of the distribution of changes of direction (klinokinesis), or the step length (orthokinensis). As shown above, these two types of regulation of the sinuosity actually lead to a similar drift of animals in the environment. In fact, the differential orthokinetic mechanism, disconnected from sinuosity regulation, i.e. taken along with a constant sinuosity movement, is not responsible for the phenomenon of animal aggregation. Furthermore, this mechanism does not seem to lend itself to any biological applications. We have not found in the literature, nor have we been able to imagine, any case where an animal can benefit from varying only its velocity in response to variations in the intensity of a stimulation.

On the other hand, the absolute orthokinetic mechanism is of great value in space-use strategies in a heterogeneous environment, consisting of areas of varying suitability with limits that are not perceptible by animals. In this patchy environment, the animals cannot therefore immediately locate the most suitable areas. An animal moving with a velocity that is a decreasing function of the suitability of its local environment increases the time it spends within the most suitable areas, and reduces the time spent travelling between them. If one considers the orthokinetic behaviour of a whole population, it emerges that this mechanism will indeed lead to an aggregation of individuals within the most suitable areas. This occurs because the time taken by animals to diffuse through a given area is inversely proportional to their velocity. For
example, if animals move twice as slowly within the suitable areas as anywhere else in the environment, the probability density of their positions in space, and therefore their mean density, will be twice as high in the suitable areas. The aggregation of animals based on an (absolute) orthokinetic mechanism is thus a simple statistical effect. This was clearly understood by Fraenkel & Gunn (1940), who made an analogy between orthokinesis and the automobile traffic inside and outside built-up areas.

In addition, in a stimulation gradient field, the orthokinetic mechanism leads animals to spend more time in the favourable part of the field, and therefore to aggregate there, than in the unfavourable part. Nevertheless, this phenomenon should not be confused with a spatial orientation effect, because there is no drift of animals in the direction of the gradient as is the case with differential klinokinesis.

**ABSOLUTE KLINOKINESIS**

Doucet & Drost (1985) and Doucet & Wilschut (1987) have attempted to clarify the properties of absolute klinokinesis and orthokinesis in various environments by identifying four types of kinesis (A, S, T and D). According to the new definition of klinokinesis proposed in this paper, it clearly appears that A-kinesis and S-kinesis are equivalent forms of klinokinesis, and that D-kinesis is a combination of klinokinesis (type S-kinesis) and orthokinesis (type T-kinesis). Using this new definition of klinokinesis, it can easily be shown that, like absolute orthokinesis, absolute klinokinesis contributes greatly to space-use strategies in a patchy environment. Indeed, when formalizing paths as first-order correlated random walks, we have expressed the expected diffusion $E(D)$ of a path having length $L$ and sinuosity $S$ by (Bovet & Benhamou 1988)

$$E(D) = 1.77 \sqrt{L/S}$$

A dynamic expression for the diffusion process is obtained by taking the product of the velocity $V$ and the travel time $T$ instead of the path length: $L = VT$. An animal can therefore increase the path length it walks, hence the time it spends, within the most suitable areas of its environment by increasing the sinuosity, and can limit the path length, hence the travel time, between these areas by decreasing the sinuosity. An animal using the absolute klinokinetic mechanism thus regulates the time it spends within the suitable areas by controlling its sinuosity as it controls its velocity when using the orthokinetic mechanism.

As in the case of orthokinesis, taking into account the absolute klinokinetic mechanism for a whole population leads statistically to an aggregation of individuals. For example, if the animals move with a sinuosity twice as great within the most suitable areas than anywhere else, the probability density of their positions in space, and therefore their mean density, in these areas will then be four times higher, because of the relationship between time and sinuosity in the diffusion equation. The diffusion is proportional to the square root of the travel time and inversely proportional to the sinuosity. Thus, absolute klinokinesis leads to spatial regulation, whereas absolute orthokinesis leads to temporal regulation of the diffusion; the joint use of these two mechanisms thus makes it possible for animals to control their diffusion dynamically.

Furthermore, it should be noted that absolute klinokinesis leads to a very slight drift of animals in a stimulation gradient field. This property was used by Jamon & Bovet (1987) to account for the homing performances of wood mice, *Apodemus sylvaticus*, released in a ‘home-like vegetation’ gradient field. However, the drift generated by absolute klinokinesis is so slight that it can be said to be a property with a very minor effect.

**APPLICATIONS OF THE MODELS**

Klinokinetic and orthokinetic mechanisms have been used to explain various spatial behaviours. For example, the model proposed by Neill (1979) to account for the behaviour of fish searching for a preferred temperature in a thermal gradient field is a differential klinokinetic model. The model proposed by Wilkinson (1952) and Smith & Shappy (1963) to account for the trans-oceanic migration of birds and salmon, which was based on a simple random walk model, can also be said to come under the heading of differential klinokinesis. Here, however, there was no stimulation gradient, sensu stricto; animals were assumed to use external cues to find the direction of their place of birth, and to regulate their movements as a function of the orientation of the step they travel in relation to this
direction, by means of the step length

\[ P_i = P_b (1 + k \cos \theta) \]

Since \( \theta \) is uniformly distributed, we have \( E(\cos \theta) = 0 \) and \( E(\cos^2 \theta) = 0.5 \), so that the efficiency of this mechanism can be easily quantified: 

\[ \frac{E(D_i)}{E(L)} = E(P \cos \theta) / E(P) = 0.5k. \]

From 500 simulated paths comprising 1000 steps with nine values of \( k \) arithmetically ranging between 0.1 and 0.9, we specified that 

\[ E(D_i) = 0.5kL. \]

Figure 3. Foraging movements of a hypothetical animal in a patchy environment. Small dots represent the position of the prey items and large dots, the position of the animal after constant time intervals. Absolute klinokinetic and orthokinetic mechanisms lead to an area-restricted searching behaviour, by increasing the time spent in areas with high prey item contents.

A similar application of the differential klinokinetic model has been provided by Jamon (1987) in connection with the 'search-loops' exhibited by some arthropods when searching for their nest. As in the previous example, the environment contains no stimulation gradient; it was assumed that these arthropods can determine the direction of their nest (by vector-navigation) from any point around it, and then regulate the sinuosity of their paths as a function of the orientation of the step they just walked in relation to the nest direction.

The differential klinokinetic model has also been used by Bovet & Benhamou (1985) and Bovet et al. (1986, 1988) to account for the movements and spatial orientation of a mammal in its home range. For this purpose, it was assumed that the home range corresponds to a radial olfactory gradient field centred on the animal's burrow: the intensity of odour decreases in any direction from the burrow. The space-use pattern of the home range obtained using this model is compatible with the existence of such a gradient, under the assumption that this mammal regularly deposits scent-marks during its movements.

Figure 4. The properties of klinokinetic and orthokinetic models, in differential and absolute modes.
conditions. An (absolute) orthokinetic model has been applied, for example, to the control of body temperature in fish (see Neill 1979). As suggested by Neill, the search for the preferred temperature in a thermal gradient field must be based on a differential klinokinetic mechanism. However, it seems likely that absolute orthokinetic as well as absolute klinokinetic mechanisms may become operative as soon as the fish reaches a preferred temperature area, to maximize the time spent therein.

One important application of absolute klinokinetic and orthokinetic mechanisms relates to foraging behaviour in patchy environments. These mechanisms allow an animal to adapt the allocation of its search effort, i.e. the time spent searching per unit of area, to the contagious distribution of prey items, by regulating its sinuosity and its velocity. Indeed, clumped prey items form temporary, non-delimited, randomly distributed patches which have no physical reality, but correspond only to a statistical concept (Arditi & Dacorogna 1988; Kacelnik & Bernstein 1988). Consequently, the currency for an animal foraging in such an environment is not to estimate the quality of the inspected patch, as in most optimal foraging models, but to decrease its diffusion in order to increase its search effort after finding a prey item, because the probability of finding other items nearby is higher than elsewhere. Let us therefore consider a hypothetical animal which increases its search effort locally in response to finding a prey item by suddenly increasing its sinuosity and decreasing its velocity, and which thereafter decreases its search effort progressively with the time elapsing since the last prey item was found. According to this simple rule of thumb, a high frequency of prey finding, indicating a high local density of items, will lead this animal constantly to increase its search effort, whereas a depleted search area will cause it progressively to adopt its initial sinuosity and velocity values, and therefore to reach another patch (Fig. 3). Note, however, that this animal must be able to estimate the heterogeneity of its environment from the temporal distribution of its findings in order to maximize its search efficiency by optimizing the way it regulates sinuosity and velocity. The adaptive role of these types of mechanisms has been underlined by numerous authors from a theoretical point of view as well as on the basis of experimental data (Murdie & Hassell 1973; Hassell & May 1974; Smith 1974 a, b; Bond 1980; Carter & Dixon 1982; Knoppien & Reddingius 1985). Nevertheless, it should be noted that these two mechanisms do not function in the same way: an increase in sinuosity reduces the search area whereas a decrease in velocity increases the probability of detecting encountered prey (Gendron & Staddon 1983; Knoppien & Reddingius 1985) and the time devoted to feeding (Arditi & Dacorogna 1988). Absolute klinokinetic and orthokinetic models can therefore be said to be useful tools for formalizing the 'area-restricted searching' behaviour which has been mentioned in the framework of optimal foraging theory (see Schoener 1971; Krebs 1973, 1978, 1979; Pyke et al. 1977; Pyke 1978, 1984).

CONCLUSION

In this paper, we have formalized klinokinesis and orthokinesis from a correlated random walk model by introducing cybernetic feed-back regulation in response to information gleaned in the local environment during a movement: they can be considered as elementary, but efficient, sensorimotor mechanisms. The distinction between the spatial and temporal control of movement, in the absolute as well as the differential mode, makes it possible to elucidate the properties of these mechanisms involved in animal aggregation, by separating what relates to spatial orientation from what relates to space use. This settles the old question about the need for sensory adaptation in the mechanisms involved in animal aggregation. We have shown that, with sensory adaptation (differential mode), klinokinesis can be seen as an elementary mechanism of spatial orientation whereas orthokinesis seems to have no biological application and that, without sensory adaptation (absolute mode), klinokinesis and orthokinesis can be seen as elementary space-use mechanisms. Animal aggregation in the most suitable areas of the environment can therefore be based on mechanisms both involving and not involving sensory adaptation (Fig. 4).

Since there exists such a wide range of potential applications for the kinetic models presented in this paper, they will certainly be able to contribute towards building a more general theory of spatial orientation and space use in animals, based on the
foundations laid by Jander (1975), Van der Steen & Ter Maat (1979), Bell & Tobin (1982) and Schone (1984). These models suggest that under some conditions animals can efficiently exploit their environment by means of elementary mechanisms which need neither spatial memory nor long-range orientation abilities.

REFERENCES


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