Simple Connectionist Models of Spatial Memory in Bees

DAVID C. KRAKAUER

BBSRC NERC Ecology and Behaviour Group, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, U.K.

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Neural network models are used to investigate the ways in which bees use landmarks to navigate through space. The snapshot hypothesis, whereby bees remember a position in space by taking an instantaneous snapshot of the configuration of landmarks, is explored using a Hebbian learning rule and a distributed memory. The number of landmarks and snapshots are shown to contribute to the accuracy of spatial memory. Lining snapshots up along lines of inspection while bees move away from a target site improves performance when estimates of distance involve perceptual errors. When the perception of distance involves scalar error, and if most snapshots are taken close to the target, bees will weight landmarks closer to the target. Networks that respond to distant landmarks can be trained to activate further networks with fine grained local representations to recall the positions of more than one goal. This latter ability compartmentalizes memory for the recollection of complex routes.

1. Introduction

Learning the unique location of an object in the spatial environment is an adaptation of enormous value to bees and wasps (Evans, 1966; Butler et al., 1970), which rely on such knowledge to successfully return to profitable foraging areas and mating stations. A number of experiments have been undertaken to analyse the behavioural components of spatial memory tasks in these insects. A feature to emerge from such studies is the key role of visual landmark cues; some important results include:

(i) Bees are able to memorize their spatial environment by making use of information provided by surrounding landmarks (Cartwright & Collett, 1983; Gould, 1987; Collett, 1992).
(ii) Bees learn the apparent size and bearing of the landmark in relation to the food source (Cartwright & Collett, 1983).
(iii) Landmark memories are stored in earth-based co-ordinates (Lindauer, 1960; Collett & Baron, 1994).
(iv) Not all landmarks are equally weighted in the goal relocation task (Cheng et al., 1987).
(vi) Bees are able to follow novel routes through their environment (Gould, 1986).
(vii) Bees can relocate several food sources along a search path (Heinrich, 1976) and employ distant landmarks as contextual cues to activate memories of “path segments” (Collett et al., 1993).

It has been suggested that bees and wasps are able to navigate through space by using a map-like representation of the environment (Gould, 1986). These internal maps “may consist of a set of landscape memories with a homeward vector linked to each memory” (Cartwright & Collett, 1987). This hypothesis is derived from a model based on “snapshot memory”. The snapshot model involves a bee taking an instantaneous recording of its spatial environment and associating this with a vector directed towards a target calculated from its current position. This target may be a food source (Price, 1975) a mating station (Alcock et al., 1977) or the home nest (Robinson & Dyer, 1993). During the process of exploring the
environment, the bee builds up a memorized “library” of such snapshots, which can be used to relocate the target from diverse positions in space. There are some features of this model worth noting. A bee’s uncertainty of its homeward vector is an increasing function of its distance to the closest snapshot, which results in the concept of a “catchment area” which is defined as the effective distance from the nearest stored snapshot a bee may travel before its certainty falls below a given performance measure. At the goal the bee is assumed to take two snapshots, one of proximal landmarks only, and one of all visible landmarks in its environment. This is thought to allow the more distant cues to activate the memory associated with the nearby landmarks. The consequence of such “filtered snapshots” involving two or more discrete representations is that a mechanism is required to activate the appropriate spatial representation. Finally snapshots are stored with reference to some terrestrial co-ordinate system.

In this paper connectionist models (see Hertz et al., 1991) are used to explore the snapshot hypothesis of landmark use in spatial memory. Connectionist models of spatial memory have been usefully applied to studies of the hippocampus (Zipser, 1985; Sharp, 1991; Shapiro & Hetherington, 1993) and to navigational strategies controlling robotic search (Miller, 1989). These models possess many of the features assumed to be important in bee spatial memory: notably, a hierarchy of representations of the spatial scene, the ability to generalize a response when faced with novel stimuli, and an incremental improvement in performance with increasing numbers of landmarks and “snapshots”. Connectionist models can be broadly categorized into two groups, those requiring the expected behaviour to be specified in advance as an aid to training (supervised learning), and those that acquire the behaviour through a learning process over a series of trials using feedback information (unsupervised learning). Here both types of model are used to explore the sensory-behavioural elements of landmark mediated spatial learning. The models do not claim to be neurobiologically accurate or attempt to address all the described spatial behaviour, they rather seek to examine the problems that bees are expected to cope with when learning to orient through space employing information from landmarks aided by a “compass sense”.

The paper is divided into three parts each with a different model aiming to explain some feature of landmark learning. The first section looks at the information provided to a model bee by different numbers of landmarks, and how the snapshot hypothesis can be realized through pattern generalization by a neural network. This leads to a discussion of how stereotyped orientation flights could have arisen as a consequence of error-prone assessment of landmark bearings. The second section addresses the observation that not all landmarks influence searching behaviour to the same extent: landmarks closer to the target appear to have a greater influence on homing behaviour than those placed more distantly. The model explores this behaviour by assuming that uncertainty over the whereabouts of landmarks will be influenced by proximity to the target position. The third section deals with learning and retrieving memories for more than one target position and presents a mechanism whereby more distant landmarks are able to serve as contextual cues to activate local area memories.

2. Snapshot Memory and the Accuracy of Spatial Memory

Bees and wasps departing from a new source of food are observed to perform orientation flights; this behaviour involves a systematic sequence of locomotor flights in the vicinity of the food source (Wehner, 1981). Collett & Lehrer (1993) analysed the structure of the orientation flights in the wasp Vespula vulgaris and found that on departure from a feeder, a wasp backs away in a series of arcs while fixating the feeder at key points which fall along imaginary lines radiating from the feeder. Collett and Lehrer suggest that wasps take snapshots during these brief inspection periods, and that by taking snapshots along a line any difference in perceived landmark position will result from scaling rather than rotation. Zeil (1993), studying orientation flights in Ceceris, called the snapshot theory of orientation flights the “multiple view hypothesis”, where snapshots taken during the inspection periods allow the wasps to sample several positions in space in order to form a more complete internal representation of the scene. Similar results have been found in honey bees by Lehrer (1993), who termed the inspections “turn back and look” behaviour. I seek to reconcile the snapshot hypothesis with a neural mechanism for pattern retrieval. Bees sample a smaller region of the environment than they can effectively navigate from and hence bees must generalize their responses to landmark cues. Generalization is a property of connectionist systems which involve high connectivity (Schwartz et al., 1990) and hence offers a hypothetical mechanism for spatial generalization in bees and wasps.
2.1. THE SNAPSHOT MODEL

The basic navigational model used to explore the workings of snapshot memory is a feed-forward network or “perceptron” (Rosenblatt, 1962) which employs distances and angular deviations from “south” to landmarks to form an estimate of its current position. At each inspection point or “snapshot” the model is provided with a set of landmark distances and angles, and is trained to produce a vector directed towards the target. The model is tested in extinction by challenging it with a set of novel landmark distances and vectors in the absence of the target and recording the vector that is generated. An error function is employed to assess the accuracy of the model’s memory (also referred to as the “model bee” or network) when trained with varying numbers of landmarks and snapshots. The spatial environment in which the network is placed is a 40 × 40 square array representing an environment with 1600 discrete locations. Landmarks are placed at strategic positions within this environment. The model bee is assumed to have a visual field capable of subtending a full 360°, so that at any point in the landscape the model bee is potentially aware of the whereabouts of the landmarks from its present position. The role of landmark number is explored by training the network to produce the desired target vector at four snapshot positions in space. At each snapshot position the output of the network is calculated by expressions (1) and (2). The network learns to produce the desired output by iterating the rules (3) and (4) 200 times for each snapshot position. This schedule is replicated for one, two and three landmarks placed in the environment, where prior to each replication the weights are initialized at zero. The model bee is tested by placing it at each discrete position in the environment in the absence of the target with the number of landmarks during testing made to correspond to the number present in the training phase. This implies that while the model bee only takes snapshots at four locations (the corners of the environment), it is required to produce a response at 1600 locations. Figure 2 illustrates in graphical terms the contents of memory as a “snapshot map” following training with one landmark. At each position in the environment is a vector directed towards a target.

![Diagram of the snapshot model](image)

**Fig. 1. Architecture of the snapshot model. Two-layer feed-forward “perceptron” which accepts polar co-ordinates from landmarks. The distance to each landmark $S_i$ and the bearings to each landmark from the north–south axis $\theta_i$ produce a weighted sum at the output unit $O$.**

The accuracy of the model’s memory (also referred to as the “model bee” or network) when trained with varying numbers of landmarks and snapshots. The spatial environment in which the network is placed is a 40 × 40 square array representing an environment with 1600 discrete locations. Landmarks are placed at strategic positions within this environment. The model bee is assumed to have a visual field capable of subtending a full 360°, so that at any point in the landscape the model bee is potentially aware of the whereabouts of the landmarks from its present location. Hence, the model bee has information on the precise whereabouts of the landmarks from its present location in polar co-ordinates $(S_i, \theta_i)$ with the bee’s body acting as the origin. Similar information is provided for a target at a distance $D$ and angle $A$ from the current position. The output of the network $O$ is calculated as follows:

$$o = \sum_i w_i S_i + \sum_i v_i \theta_i,$$

and is subjected to the squashing function

$$O = \tanh(o),$$

where $w_i$ and $v_i$ are the weight vectors connecting the inputs to the outputs. The output $O$ specifies the angular deviation from south given the model’s present position. The learning task for this network is, given a configuration of landmarks at a snapshot, to generate an output which produces a unit vector directed towards the target (target vector). In other words, we require that the output $O$ is equal to the polar angle from NS (polar axis) to the target $A$. We are able to find the correct mapping by modifying the weights employing the perceptron learning rule (Rosenblatt, 1962) which follows the biologically reasonable hypothesis of Hebb (1949) that each weight is added to in proportion to the product of the input and desired output. Hence weights are modified by taking

$$w_i(t + 1) = w_i(t) + \eta(A - O)S_i,$$

and

$$v_i(t + 1) = v_i(t) + \eta(A - O)\theta_i,$$

where the parameter $\eta$ is the learning rate (= 0.4).

2.2. INFORMATION FROM LANDMARKS

The role of landmark number is explored by training the network to produce the desired target vector at four snapshot positions in space. At each snapshot position the output of the network is calculated by expressions (1) and (2). The network learns to produce the desired output by iterating the rules (3) and (4) 200 times for each snapshot position. This schedule is replicated for one, two and three landmarks placed in the environment, where prior to each replication the weights are initialized at zero. The model bee is tested by placing it at each discrete position in the environment in the absence of the target with the number of landmarks during testing made to correspond to the number present in the training phase. This implies that while the model bee only takes snapshots at four locations (the corners of the environment), it is required to produce a response at 1600 locations. Figure 2 illustrates in graphical terms the contents of memory as a “snapshot map” following training with one landmark. At each position in the environment is a vector directed towards a target.
Fig. 2. A “snapshot map” indicating the estimated target vectors produced by the model for each discrete position in the environment. The filled circle represents the position of the landmark.

which is placed centrally. The vectors are calculated from the output of the network by generating NS and EW components from the output angle \( O \) where the components are calculated relative to the current body position.

2.3. ERROR-PRONE ASSESSMENT

It is unrealistic to assume that bees are able to assess perfectly the distances and angles to landmarks and targets from a snapshot. It is rather more likely that Weber’s law applies, where scalar errors are made in assessing these values, with the magnitude of the errors proportional to the distance. Weber’s law may be formulated as

\[
k = \frac{\Delta I}{I},
\]

where \( k \) (the Weber fraction) is the ratio of a stimulus \( I \) to the change in stimulus intensity \( \Delta I \) required to result in a perceptible difference. Perceptual error may be incorporated into the model by presenting perceived angles \( \theta^p \) and perceived distances \( S^p \) to the network in place of the actual angles and distances. We let these perceived values equal

\[
\theta^p, \text{ which is a random variable sampled from a } N(\hat{\theta}, \sigma^2) \text{ distribution}
\]

and

\[
S^p, \text{ which is a random variable sampled from a } N(S, S\gamma) \text{ distribution}
\]

where \( N(\mu, \sigma^2) \) is the normal distribution with a mean \( \mu \) a standard deviation \( \sigma \) and coefficient of variation \( \gamma \). From expressions (6) and (7) it will be apparent that there is scalar error in distance and a non-scalar Gaussian error in angle. There is no good reason to expect that angles should involve scalar errors, since larger angles do not imply that a greater demand is placed on perception. Hence, by increasing the distance the error in estimating distance is increased, and by increasing the coefficient of variation the accuracy in distance perception is decreased.

In order to assess the fidelity of memory at novel positions in the environment, an error function is constructed. This function returns a scalar value which represents the average deviation of a network’s calculated output angle \( \theta^o \) from the desired target angle \( \theta^t \) for every permissible position in space:

\[
\chi = 1 - \frac{\sum \sum |\theta^o - \theta^t|}{1600}.
\]

If the memory were perfect at every position in space, or more precisely, if the memory at each point in space formed a perfect target vector, then the value of \( \chi \) would be 1. It should be stressed that this is simply one convenient way of assessing the accuracy of memory at novel positions in the environment.
Figure 4. Ordered (a) and random (b) snapshot configurations. The large open circle represents the landmark; the square the target and the small circles with target vectors represent the positions at which snapshots are taken.

of memory, for one can imagine cases where few vectors are equal to the target vectors and yet a short path to the target remains available. It follows that the absolute value of function (8) is not particularly significant but that the trend it expresses reveals the contribution of spatial information.

Figure 3 is a plot of accuracy ($\chi$) against variance ($\sigma^2$) for one, two and three landmarks. When the variance ($\sigma^2$) in the distributions which generate the perceived angles and distances is zero, minimal information is provided by different numbers of landmarks. Hence if bees were able to perfectly perceive landmark distances and landmark angles, only one visible landmark would be required for spatial navigation (as assumed in Fig. 2). But as errors in perception increase so does the amount of information provided by increasing numbers of landmarks. At a variance of 1 three landmarks provide a significantly more reliable means of navigating to a target than one or two landmarks.

The foregoing results indicate that landmark numbers influence the information available for learning the target position. We now turn to snapshots. The observations of Collett & Lehrer (1993) on Vespula show that snapshots are precisely regulated and radiate out from the target falling along two lines of inspection. To test for the effects of regularity in inspections on memory, two seven-snapshot scenarios are analysed. These test cases are shown in Fig. 4. The first [Fig. 4(a)] is where snapshots fall along two lines radiating out from the target, while the second has the snapshots randomly distributed to fill the space below the target [Fig. 4(b)]. For each test configuration the network is trained with rules (3) and (4) through 200 iterations at each snapshot position. In Fig. 5 the accuracy of spatial memory, when tested following training with the ordered configuration [Fig. 4(a)], is plotted for increasing numbers of snapshots (one through to seven inclusive) where inputs are perfect ($\sigma^2 = 0.0$) or perceived with error ($\sigma^2 = 0.5$). In other words, the network is trained and tested with one snapshot (position 1), two snapshots (position 1 and 2) up to seven snapshots. Accuracy increases with increasing numbers of snapshots but the greatest increase comes for between three and four snapshots. Accuracy where training and testing involves perceptual errors consistently falls below those involving perfect assessment, whereas the qualitative trend remains the same. These results should not be interpreted too literally. The precise form of Fig. 5 is, in all likelihood, a consequence of the structure of the network. However, the results do imply that there should be a non-linear contribution to memory by snapshots,
where at high and low snapshot numbers the improvement in memory following additional snapshots will be marginal.

Figure 6 shows the results of training and testing with the full number of seven snapshots on the ordered [Fig. 4(a)] and random [Fig. 4(b)] training configurations. When perception does not involve errors the ordered and random configurations do not differ in their accuracy. When perception is error-prone the ordered snapshots produce a significantly more accurate spatial map than the random configuration.

3. Effects of Target–Landmark Distance on Landmark Weighting under Error-prone Perception

The landmarks that bees use to navigate through space are not all equally important. Landmarks positioned closest to the goal are observed to preferentially direct searching behaviour (Cheng et al., 1987). Cheng et al. (1987) present two hypotheses to account for this fact. The first suggests that bees possess a mechanism that scales the magnitude of target vectors according to the distance between landmarks and the goal in a snapshot. Searching will be guided by those vectors with the greatest magnitude which will be found by those landmarks closest to the goal. The second hypothesis assumes that search time is an increasing function of the goodness of fit between snapshot and retinal image (this corresponds to the polar inputs in the present model), where the goodness of fit calculation includes a weighting term. Both of these hypotheses assume a mechanism directly responsible for weighting. The possibility exists that landmark weighting is an observational phenomenon only: the product of a process where weighting is not an integral part but a result. This second section explores the hypothesis that where there are scalar errors, the magnitude of an associative response may diminish. Landmarks far from the target present to the network a distribution of possible distances rather than a single distance as in the previous section. If we additionally assume that snapshots are taken principally from nearby the target, there will be greater uncertainty about the whereabouts of landmarks far from the target.

We wish to examine the behaviour of a model bee trained with a target placed close to one of two landmarks. Testing configurations will then present paired down versions of the training configurations where only one of two landmarks is presented to the model bee. Since the test pattern is partial, the model should be uncertain as to how it should interpret the single landmark: either as the one that lay closest
Fig. 7. Testing for the influence of perceptual error on landmark weighting. (a) Training environment showing two training configurations. Filled squares = landmarks, hatched squares = targets, filled circles = snapshots. To the left is configuration I where the target lies south of the left landmark and north of the right landmark. In configuration II this is reversed. During training only one configuration is present. (b) Surface plot of most frequently visited areas when tested with one landmark positioned as shown (filled square) following training with configuration II. (c) Surface plot of most frequently visited areas when tested with one landmark positioned as shown (filled square) following training with configuration I.

to the target or the one that lay furthest from the target. In Fig. 7(a) the positions of the two landmarks are marked as solid squares. The hatched squares denote the positions of the targets, which lie close to each of the two landmarks. The small filled circles are the positions at which snapshots are taken corresponding to the nearby targets (two targets and six snapshots are shown on the one illustration for convenience only and do not reflect training where only one of the targets, three adjacent snapshots and two landmarks are used). During training the three snapshots closest to the target present receive 200 iterations of learning through functions (3) and (4), while distances and angles are perceived with an error of $\sigma^2 = 0.5$. During testing one landmark is placed in the centre of the environment. To simulate ambiguity following presentation with a single landmark, all of the input units ($i = 1, 2$) are stimulated with the distances and angles from this landmark, and hence the network is torn between producing a target vector consistent with one of the two landmark positions during training. In other words, should the model bee direct itself to the right of the landmark (south) consistent with snapshots taken close to the northern landmarks (configuration I) or to the left of the landmark (north) consistent with snapshots taken close to the southern landmark (configuration II)? Figures 7(b) and (c) are plots of the most frequently visited areas in the environment. These surface plots are produced by starting the network in each of the discrete environmental "grid points" and moving the network according to the target vectors calculated from memory and landmark input. Twenty steps are taken from each starting position. The surface therefore depicts those points to which the model bee tends most frequently.

Figure 7(b) is generated following training with configuration II and Fig. 7(c) with configuration I. In each case, the most frequently visited areas are those consistent with the landmark placed closest to the target. In Fig. 7(b) the model bee explores north of the landmark; the relative position of the target in training with configuration II. In Fig. 7(c) the model bee explores south of the target, the position of the target in training configuration I.

4. Constructing Path Segments through Competitive Learning

Bees will often visit more than one target site during a foraging trip. Collett et al. (1993) analysed sequence learning behaviour in *Apis mellifera*. These bees were trained to learn a route through a series of obstacles, where the bees were able to learn a complex path stopping at many sites. The order in which sites were visited did not appear to significantly affect performance. Collett and co-workers were led to conclude that each site was memorized as an independent path segment. Each path segment is a memory
of one target site constructed using local landmark configurations. These segments become linked together to form a route. They suggested that these segments may be linked by a predefined motor sequence, a temporal pattern, or become activated by external signals in the environment. In this section the latter case is explored.

4.1. HIERARCHICAL SNAPSHOT MODEL

If a bee were allowed to learn multiple targets, a mechanism would be required to activate the memory for each target site in the correct context. If one assumes that bees take a filtered snapshot at the target in which only distant landmarks are recorded, each target site stands in a unique position in relation to these landmarks. If one also assumes that errors are made at assessing these distances, then distant landmarks will delimit “catchment areas” rather than single points. Landmarks closer to the target will be required in order to increase the precision of representation. This hierarchy of response suggests that a hierarchical mechanism may play a part. The model of this section is a proposed mechanism for activating distinct snapshot models in different regions of the environment. The architecture of the hierarchical model is illustrated in Fig. 8. The top layer of the model is an array of snapshot models, with one snapshot model used per target learnt. These snapshot models receive an input which has filtered out snapshot model used per target learnt. These snapshot models receive an input which has filtered out landmarks only ($d$istant cues and contains information about local shot models receive an input which has filtered out snapshot model used per target learnt. These snapshot models are an array of snapshot models, with one model is illustrated in Fig. 8. The top layer of the environment. The architecture of the hierarchical mechanism may play a part. The model is placed at one target site and allowed to take a filtered snapshot of the distant landmarks. The network is trained using the competitive learning rule of Rumelhart & Zipser (1985). When stimulated with an input pattern from the distant landmarks, only the output unit with the largest net input is activated. Where $L_j$ are the distances to the distal landmarks, $z_j$ the angles, and $u_{jm}$ and $t_{jm}$ the weights to the output units, $P_{m*}$, the winning unit is denoted thus

$$P_{m*} = \sum_j u_{jm} L_j + X_1 + \sum_j t_{jm} z_j + X_2 > 0$$

$\sum_j u_{jm} L_j + X_1 + \sum_j t_{jm} z_j + X_4$ (for all $j$). (9)

The weights to the winning unit are updated using the following rules

$$u_{jm}(t+1) = u_{jm}(t) + \lambda p_{m*}(L_j - u_{jm}(t)),$$ (10)

and

$$t_{jm}(t+1) = t_{jm}(t) + \lambda p_{m*}(z_j - t_{jm}(t)).$$ (11)

where $\lambda$ is a learning rate parameter ($=0.6$), and the $X_i$ are continuous random variables sampled from a uniform distribution between 0 and 1. These random variables are introduced to encourage competition between the output units following stimulation with novel inputs, hence breaking any symmetry between units. This rule increases the weights to the winning output unit for a given input vector when the weight values are less than the normalized distances, and decreases the weights when the distances are greater than the weights. The effect of the rule is to cause the value of the weight vector to the winning unit to become equal to the normalized distances to the input terminals of the network. This causes the input patterns to be divided into patterns of output unit activation according to regular features in the input. These regular features correspond to positions in the environment with greatest spatial affinity. The model is placed at one target site and allowed to take a filtered snapshot of the distant landmarks. The network is trained using the competitive learning rules [[(9) and (10)]] to produce an activation pattern for the inputs at that point. In other words, the distances and angles on the input units when fed forward through the network cause one of the two output units to become active. This activates the snapshot model to which it is connected. The local landmarks at this point can then be learnt using a snapshot model with multiple inspection points—a process identical to that

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**Fig. 8.** Architecture of hierarchical snapshot model. Competitive learning module at bottom receives filtered input from distal landmarks. This causes activation of one of the two snapshot models via the activation pathways $A_1$ or $A_2$. Each snapshot model receives filtered inputs from the proximal landmarks and learns the position of one target.
discussed in Section 2. The model is forced to take a snapshot at the second target, which again involves evaluating the outputs using expression (9) and training the weights with (10) and (11) for the new inputs. This causes the untrained output unit to become active in the second position. The competitive learning network will then generalize responses for unvisited positions in the space between the two snapshots.

4.2. A TWO-TARGET SNAPSHOT MODEL

The model bee was trained to learn the positions of the two target sites shown in Fig. 9. The environment has a total of six landmarks, two of which are placed at the vertices of the environment (distal landmarks). The remaining four are divided into two groups of two positioned around the two target sites. The hierarchical model is placed on one of the target sites and the competitive network receives input from the four distal landmarks. Learning rules (10) and (11) are used to update the weights to the winning output unit (9) through 150 iterations of training. The snapshot model, activated by the output from the competitive network, is trained to learn the local landmarks as in Section 1. The hierarchical model is then placed on the second target site and trained for these new inputs using both the competitive rule to distal landmarks and snapshot model to local landmarks. Figure 9 illustrates how the environment has been divided up into two patterns of activation. When the hierarchical model is placed in the bottom region, the snapshot model that has learnt the target for that region is activated. When the model is placed in the top region the other snapshot model is activated. The hierarchical model effectively uses the distal landmarks as contextual cues to activate a more fine-grained memory of space. For a network with $n$ output units, the inputs will be divided into $n$ stimulus patterns. The competitive learning rule therefore provides a mechanism for constructing routes of $n$ independent path-segments when the environment can be divided up into patches. Each of these patches should be rich in landmarks and spaced further apart from each other than their inclusive landmarks.

5. Conclusions

The results from the models allow the following points to be made:

1. The snapshot hypothesis, whereby space is sampled at discrete points in order to memorize the configuration of landmarks at these points, is given a mechanistic explanation by constructing a connectionist model. This model builds an egocentric map of its environment and, through a process of induction or “generalization”, is able to navigate from unexplored positions where these positions show some resemblance to those at the snapshot.

2. The map of space becomes more accurate as the number of landmarks and snapshots increases. Specifically, more snapshots reduce uncertainty by reducing the total unexplored area, while more landmarks reduce error by providing more information at each point.

3. When bees make scalar errors in assessing distances and Gaussian errors in estimating bearings to landmarks, positioning snapshots along lines radiating from the target improves recall over snapshots positioned at random. This result is true even when test inspections are not restricted to the points on which snapshots were taken.

4. Errors in perception imply that memory only imperfectly matches the true state of the world. This error is likely to increase in proportion to the stimulus magnitude (Weber’s law). If snapshots are concentrated around the target and some landmarks lie closer to this target than others, then memory for this target is more accurate when predicated on these adjacent landmarks than landmarks positioned further away. Hence, if there is ambiguity over the identity of a landmark, on average this landmark will produce a response consistent with the target being positioned close by.

5. A feature detection rule (a rule that divides inputs into sets sharing common properties) is able to
divide space up into regions according to a bee’s position in relation to the configuration of distant landmarks. Such a rule can form the basis of a mechanism that activates “path segments” or additional networks which can then respond to local landmark configurations. This allows memory to become compartmentalized for the recollection of complex routes.

Snapshots provide information to a bee by providing a set of vantage points sufficiently representative of the environment that it becomes possible to interpolate or extrapolate from experience responses for unvisited positions in space. More snapshots provide increasing information but at a diminishing rate (Fig. 5). We must therefore assume that snapshot numbers are limited by non-spatial considerations such as energy and time costs. Indeed Smidt Hempel et al. (1985) were able to predict bee patch leaving times based purely on energetic considerations where bees were hypothesized to maximize their net energetic gain per unit of energetic expenditure. One should also stress that increasing the number of landmarks increases performance as a function of the levels of perceptual error. Much of the animal navigation literature has neglected to examine these constraints and their consequences (but see Lehrer & Srinivisan (1993) for a discussion of the role of edge detection in target recognition). It is quite likely that different groups experience distinct degrees of error. Compare, for example, Séguinot et al.’s (1993) path integration experiments with golden hamsters with Müller & Wehner’s (1988) experiments with desert ants. These experiments suggest that search paths which involve loops passing back over the point of departure may lead to different kinds of errors in these two animals. It seems, therefore, that while the qualitative features of navigation may be general, there is unlikely to be a unitary explanation of the landmark or snapshot numbers required by all navigating species.

Errors can be reduced by sampling from points which share some common features. Hence, placing snapshots along lines which radiate out from a target cause points with the same angular inputs to be repeatedly sampled. If there is perceptual error in the inputs, this will cause the error to become averaged out. In other words, from the central limit theorem, each additional snapshot along a line reduces the standard deviation of the error by

$$\sqrt{n + 1} - \sqrt{n} \over \sqrt{n} \sqrt{n + 1}.$$  

where \( n \) is the number of snapshots falling on a single line. This function for stereotyped snapshot configurations is more general than that suggested by Zeil’s findings with Trigona, where bees favour return paths which lie close to the orientation flight path. This result implicitly states that reliable information at a few points is more helpful than noisy information at numerous points.

Whether bees weight landmarks close to the goal depends on errors in perception and taking more snapshots in the vicinity of the target or goal. Lehrer’s (1993) observations of the orientation flights of bees and Collett & Lehrer’s (1993) observations of a similar behaviour in wasps, both suggest that snapshots occur more frequently by the goal. These observations, when coupled with scalar error in distance perception, can lead to landmarks close to the goal guiding subsequent navigation. The mechanism proposed by Cheng et al. (1987) to account for this apparent weighting need not be invoked for the simple case presented in Section 3. In other words, uncertainty over the whereabouts of distant landmarks can cause search to be guided by the more familiar close landmarks. In the terms of the model, the network is incapable of producing the desired output when the input set is highly variable.

If we accept that perception is constrained and distant landmarks provide less accurate information than near ones, then distant landmarks are only able to delimit regions, while local landmarks can describe more precise points. (Collett & Kelber, 1988). The hierarchical snapshot model makes use of this observation by employing distant landmarks as contextual cues to activate fine-grained snapshot memories. Multiple target sites can be encoded in such a model if the contextual cues can be partitioned along structural lines. If the model is caused to become confused about the position of contextual cues, it will retrieve memories inappropriate for a given target. One way of explaining this model is that the distant landmarks create an expectation for a specific configuration of local landmarks. Dyer & Gould (1981) have demonstrated that bees use large-scale features of the terrain to return to a hive. Gould (1986) has shown that this ability involves more than a memory of points connected together to form a fixed route. Large-scale metric maps might result from path segments being conditionally activated by prominent features in the environment. The hierarchical model presents a mechanism for such activation, where target sites need to be visited but in no particular order. It is assumed that once a bee has encountered a target, the current path segment will be inhibited and thus allow for activation of an alternative snapshot memory. A consequence of such inhibition will be the activation of the segment placed closest to the
currently occupied segment. The precise form of this inhibition will be important in prescribing a complex route but this process is not explored here.

A few words should be said about the assumptions behind the connectionist approach and whether models of this type are at all valid if they are not maximally biological. Currently, the state of knowledge concerning the storage of spatial information is highly speculative. Studies of the relative volume of the mushroom bodies in insect species with sophisticated visual memory are shown to have well-developed areas associated with visual inputs (Howse, 1974). And while detailed anatomy of the mushroom body is available (Mobbs, 1982), it still remains unclear how these structures should relate to spatial processing. In the absence of this information, is such modelling premature? Churchland & Sejnowski (1994) defend such models on the grounds that learning in nervous systems is likely to be described by a cost function, and that rules such as those employed in this paper are grounded in similar principles. While details of the “optimization” will differ, the error surface will be similar. Furthermore, the Hebbian rule is supported by studies on long-term potentiation (Lisman, 1989) and is appealing for its ability to construct a global organization based on a local rule. Such models provide a platform for understanding the behaviour rather than offering insights into the physiology.

Finally, there is more than one mechanism which can be invoked to explain the acquisition and retrieval of spatial memories. Wehner and Srinivasan (1981) have studied the ways in which cataglyphid ants employ path integration to return to the nest following a foraging trip. Kirschfeld et al. (1975) demonstrate how insects may derive compass information from patterns of polarized light. The simplest mechanism is to select a prominent landmark and move towards it—if the target is on the landmark this is an adequate navigating mechanism (Gallistel, 1990). This paper does not deny these other mechanisms operate in spatial tasks, it rather aims to investigate what information can be gleaned from landmarks when accompanied by a compass sense.

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REFERENCES


