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# A neural-network reinforcement-learning model of domestic chicks that learn to localize the centre of closed arenas

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Previous experiments have shown that when domestic chicks (*Gallus gallus*) are first trained to locate food elements hidden at the centre of a closed square arena and then are tested in a square arena of double the size, they search for food both at its centre and at a distance from walls similar to the distance of the centre from the walls experienced during training. This paper presents a computational model that successfully reproduces these behaviours. The model is based on a neural-network implementation of the reinforcement-learning actor–critic architecture (in this architecture the ‘critic’ learns to evaluate perceived states in terms of predicted future rewards, while the ‘actor’ learns to increase the probability of selecting the actions that lead to higher evaluations). The analysis of the model suggests which type of information and cognitive mechanisms might underlie chicks’ behaviours: (i) the tendency to explore the area at a specific distance from walls might be based on the processing of the height of walls’ horizontal edges, (ii) the capacity to generalize the search at the centre of square arenas independently of their size might be based on the processing of the relative position of walls’ vertical edges on the horizontal plane (equalization of walls’ width), and (iii) the whole behaviour exhibited in the large square arena can be reproduced by assuming the existence of an attention process that, at each time, focuses chicks’ internal processing on either one of the two previously discussed information sources. The model also produces testable predictions regarding the generalization capabilities that real chicks should exhibit if trained in circular arenas of varying size. The paper also highlights the potentialities of the model to address other experiments on animals’ navigation and analyses its strengths and weaknesses in comparison to other models.

**Keywords:** animal navigation; internal representation of walls’ features; attention processes

## 1. INTRODUCTION

Animals in the wild often exhibit remarkable capabilities to return to specific places important for their survival and reproduction, such as nests, feeding places, cache sites and mating places, from the position they currently occupy in the environment (see Trullier *et al.* (1997) for an extensive review).

A long debated hypothesis regarding animals’ navigation holds that animals store information on environment in the form of *cognitive maps* (Tolman 1948; O’Keefe & Nadel 1978; Cheng 1986; Poucet 1993). Cognitive maps are internal representations that encode the geometric relationships existing between relevant objects in space, such as landmarks and goals (Gallistel 1990). Wang & Spelke (2002) observe that, in their most sophisticated form, cognitive maps encode information that is *geocentric* (i.e. based on an absolute reference system), *enduring* (it does not change with respect to time and circumstances) and *comprehensive* (it encodes all aspects that might be

relevant for navigation). On the contrary, other researchers (Gibson 1979; Trullier *et al.* 1997; Franz & Mallot 2000; Wang & Spelke 2002) support the idea that animals store information for navigation that is *egocentric* (based on a reference system centred on the subject), *dynamic* (representations change in time and are framed by the navigation task) and *limited* (animals tend to memorize only an environment’s features relevant to achieve the goal with the specific navigation process adopted).

A first approach used to empirically investigate the ways in which animals store and use information for navigation is to train and test them in partially disorienting environments. These experiments have been performed with different animal species, including fishes (Sovrano *et al.* 2002), birds (Vallortigara *et al.* 1990) and primates (Gouteux *et al.* 2001); the most studied species have been rats (Cheng 1986; Gallistel 1990; Dudchenko *et al.* 1997). For example, Cheng (1986) trained some rats to search for food in one corner of a rectangular arena. After being disoriented, the rats searched for food both at the correct corner and at the corner at a symmetrical position with respect to the centre of the arena. These results were interpreted as supporting the existence of brain modules

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specialized in encoding and processing geometric relationships between landmarks, such as the walls of the arena. Some physiological experiments with rats engaged in navigation tasks in rectangular arenas complemented these results by showing that the so called 'place cells', located in the hippocampus (O'Keefe & Dostrovsky 1971), fire in correspondence to places in the arenas situated at specific distances from walls (O'Keefe & Burgess 1996).

Another common approach used to study how animals encode information used for navigation consists in training them in specific conditions and then testing them in partially modified conditions: the generalizations and errors exhibited by the subjects give important indications on the way they organize and use information on the environment. Cartwright & Collett (1983), for example, trained bees to search a food target set at a particular position with respect to three cylindrical landmarks, and then tested them with landmarks set at double distances from the target: the results showed that the bees searched the target at a position where the relative directions of the landmarks had not changed. Collett *et al.* (1986) trained gerbils to search for food set at a specific position with respect to two or three cylindrical landmarks, and then tested them after having increased the distance between the landmarks. The test with two landmarks (more relevant for this paper) showed that the gerbils searched the target in two places, each corresponding to the position of the food with respect to only one of the two landmarks experienced during learning (note that gerbils have a non-visual direction sense).

Another approach relevant for understanding how animals store and use information for navigation, that also includes the experiments targeted in this paper, investigated the capability of different animal species to learn abstract rules about the geometric relationships existing between landmarks and goals. In particular, some of these studies focused on the capacity of animals to abstract the concept of *centre* between different arrays of landmarks. Kamil & Jones (1997), for example, first trained Clark's nutcrackers (a corvid species) to search for food located at the central position between two cylindrical landmarks arranged at different distances in different trials and then tested them with landmarks set at novel distances (interleaved with the previous ones). In the new conditions, the birds continued to search for food at positions situated midway between the landmarks, so exhibiting the capacity of abstracting the notion of centre. Spetch *et al.* (1997) carried out similar experiments with pigeons and humans. The subjects were first trained to search a target located at the central position between arrays of landmarks. When tested with landmarks set at increased distances, humans selected a position situated at the centre of the array, while pigeons selected places situated at a position corresponding to the position with respect to only one landmark that the target had during learning. Tommasi *et al.* (1997) and Tommasi & Vallortigara (2000) carried out similar experiments with domestic chicks trained to search for food at the centre of closed arenas. Being targeted in this paper, these experiments are now illustrated in detail.

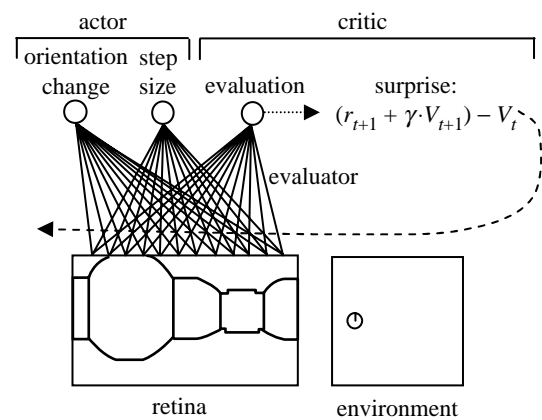
Tommasi *et al.* (1997) first trained some chicks to search for food hidden in sawdust at the centre of a square arena with sides measuring 70 cm and surrounded by wooden walls with a height measuring 40 cm, and they then tested them in the arena used for training and in a square arena with sides measuring 140 cm, both without food. In these tests, in the small arena chicks searched for food at the centre of it while in the large arena they searched at the centre of it *and* at locations that had a distance from the closest walls equal to the distance of the centre from the walls experienced during training (i.e. about 35 cm). The authors repeated these experiments using circular arenas with diameters measuring 70 cm (training and testing) and 140 cm (testing). In the tests with the small arena, chicks searched for food at the centre of it, but interestingly, in the large arena they searched for food *only* at a distance of about 35 cm from the closest walls.

The authors interpreted these results as suggesting that chicks searched for food at about 35 cm from walls in the larger arenas because, during training, they had memorized the location of the target in terms of specific distances from walls. The authors also suggested that chicks estimated distances from walls on the basis of the perceived 'angular size of the walls' height' (the larger this height, the closer the walls). The explanation of the fact that chicks searched for food at the centre of arenas with large size was more problematic but interesting at the same time. Tommasi *et al.* (1997) argued that: '(the chicks) were able to take into account the fact that the relative distances between certain points located on the walls and the centre should be equal. (...) Apparently, identifiable landmarks such as corners were needed to compute this centre because chicks were unable to localize it in transfer tests using circular arenas'. However, the results of experiments did not allow the authors to specify which 'points located on the walls' were used by chicks to equalize the distances from walls, nor to specify better the role played by corners.

Tommasi & Vallortigara (2000) replicated the experiments with square arenas and carried out some other experiments, not discussed further here, where the height of walls was manipulated to investigate its role in chicks' behaviour. In this paper, the authors seem to suggest that chicks evaluated distances from walls on the basis of their *perceived height*, even if they still have residual doubts on a possible role played by vertical edges: '(chicks) seem to encode both absolute and relative distances (...) What sort of mechanisms do chicks actually use for estimating distances? A plausible candidate would be the angular size of environmental features such as the walls (...) (Previous studies suggested that corners are likely to be used as distinctive features to perform such a spatial equalization; see Tommasi *et al.* 1997)'. With respect to these interpretations, it is relevant to consider that Tommasi & Vallortigara (2001) replicated the tests with the small and large square arenas with monocular (eye-patched) chicks. In the transfer test in the large arena, left-eyed chicks mainly searched at its centre while right-eyed chicks mainly searched at 35 cm from walls. These results suggest that different cognitive processes might take place in the left and right

The rest of the paper is organized as follows. Section 2 illustrates the features of the simulated environment and the controller of the simulated chicks. Section 3 presents the results of the experiments carried out with the model showing, in particular, the role played by information relative to walls' features (e.g. horizontal and vertical edges, surfaces, position of vertical edges in space, etc.), and possibly by attention processes, in chicks' navigation behaviours. Section 4 presents some empirical predictions of the model relative to an experiment, not yet carried out with real chicks, where simulated chicks are trained with circular arenas of different sizes. Section 5 presents a critical comparison of the model with other computational models, and shows the potential of the former to contribute to disentangling some of the theoretical issues presented above. Finally, §6 draws the conclusions.

The simulated experiments were based on square and circular arenas with sides and diameters measuring 70 or 140 cm (with the exception of §4 that uses arenas with different sizes). The food was represented by a circular area



Chicks had a two-dimensional retina covering  $360^\circ$  horizontally and  $120^\circ$  vertically, and a viewpoint situated at their centre, as shown in the bottom graphs of figure 1. Note, from this figure, that (i) the middle point of the  $360^\circ$  horizontal dimension of the retina was set to correspond to the preferential direction of motion of the chicks set to correspond to the direction of motion of the chicks and (ii) vertical edges of walls project straight segment images on the retina, while horizontal edges project bent segment images on it as their points are at different distances from the chicks. The horizontal wide range of the retina view was thought to cover the real chicks' binocular vision field, ignoring the effects of the two eyes' overlapping region and assuming that the posterior blind spot does not produce any effect on the behaviour of real chicks as they continuously scan the environment on the horizontal plane by rotating the head around its vertical axis. The retina was composed of  $80 \times 50$  pixels. Retina pixels were activated (i.e. set at 1) by the view of *vertical and horizontal edges* of walls, and in some experiments by their *surfaces* (in §3c), but they were not activated by the arenas' ground and by the environment external to the arena. The specific pixels activated by these stimuli were computed on the basis of their geometric projections on the retina thought of as the external surface of a cylinder centred on the chicks' viewpoint. The procedure that was used to perform this computation can be sketched as follows: (i) 80 points on the walls were found by finding the intersections of walls with 80 horizontal equidistant rays exiting the chicks' viewpoint and distributed over the  $360^\circ$  of the retina (each point corresponded to a column of pixels of the retina), (ii) the



projections of the vertical edges on the retina were computed on the basis of their position with respect to the rays on the horizontal plane, (iii) the distances from the chicks' viewpoint to the 80 points on walls were computed, and (iv) these distances, the height of walls and the vertical range of the retina were used to compute the projections of horizontal edges on the retina and to activate the corresponding pixels.

At each simulation cycle, chicks selected and executed an action having the following components: (i) a change of orientation, from  $-60^\circ$  to  $60^\circ$  and (ii) a forward step, from 0 to 5 cm (when the chicks would have hit a wall on the basis of this action, only the orientation change was actually executed in the environment).

The controller of the simulated chicks (figure 1) was based on a neural-network implementation (cf. Baldassarre & Parisi 2000) of the actor-critic reinforcement-learning model (Barto *et al.* 1983; Sutton & Barto 1998). This model was chosen from among the several available reinforcement-learning models because it has a considerable biological plausibility. In particular, the model has several correspondences with the anatomy and physiology of *basal ganglia*, some deep nuclei of the vertebrate brain (Kandel *et al.* 2000). For example, Houk *et al.* (1995) suggested that computations similar to those performed by the *actor* might be implemented by the portion of the *striatum* (the input component of basal ganglia) named *matrix*, involved in the selection of actions. Moreover, the same authors suggested that computations similar to those performed by the *critic* might be implemented by portions of the striatum named *striosomes*, which play an important role, via dopamine cells, in the learning processes of basal ganglia. Indeed, with regard to the latter point, electrophysiological recordings of dopamine cells in monkeys engaged in reinforcement learning tasks showed that they have an activation pattern in time that resembles the pattern of the critic's signal in similar tasks (Schultz *et al.* 1997). Furthermore, the model was shown to be able to reproduce many behavioural phenomena involved in classical and instrumental conditioning (the experiments illustrated in this paper are an example of this; see also Sutton & Barto 1981; Balkenius & Moren 1998; Baldassarre & Parisi 2000).

The actor-critic model implemented here is now presented from an intuitive perspective (see Sutton & Barto (1998) for a more mathematically sound presentation) and ignoring the important problem of *perceptual aliasing* (Whitehead & Ballard 1991), regarding the fact that chicks' internal representations often confound external world states (e.g. different places in the arena may project similar or the same walls' images on the retina) as this did not affect the results reported here. The model is mainly composed of two neural components, an *actor* and a *critic* (see figure 1). In general, the model is capable of learning to select appropriate actions in order to maximize the *sum of the future discounted rewards* ('discounted' means that the same reward is given less importance if received later in time, see equation 2.2): the actor learns to associate suitable actions with the perceived states of the environment on the basis of the critic's 'judgment'; the critic learns to associate evaluations with single visited states on the basis of the rewards experienced after these visits, and produces a *one-step judgment* of the actor's actions on the basis of the evaluations of couples of states visited in sequence. These processes are now illustrated in more detail.

The actor is a two-layer feed-forward neural-network that takes the activation  $x_i$  of the pixels of the retina image as input and returns the chicks' actions through two sigmoid

units as output. In particular, the activations of the actor's output units are used as the centres  $\mu_j$  of two Gaussian probability density functions  $\sigma$  having standard deviation  $\rho_j$  (here both set at 0.4). These functions are then used to draw randomly two numbers mapped onto the chick's orientation change and step size (the Gaussian's tails are cut at zero and unity by redrawing new numbers when this range is violated):

$$\mu_j = \frac{1}{1 + e^{(-\sum_i w_{ji} \cdot x_i)}}, \quad (2.1)$$

$$y_j = \sigma(\mu_j, \rho_j),$$

where  $w_{ji}$  are the actor's weights.

The critic is composed of two sub-components: a neural-network that evaluates states (here named 'evaluator') and a component that computes the *TD-error*, also named 'surprise' (even if not shown here, this second component can easily be implemented neurally, see Baldassarre & Parisi 2000). The evaluator gets the retina image as input, and returns as output, through its linear unit, an *estimation* of the *theoretical evaluation* of the state related to that image. This theoretical evaluation is defined as the sum of the expected discounted future rewards:

$$V_\pi[s_t] = E_\pi[r_{t+1} + \gamma \cdot r_{t+2} + \gamma^2 \cdot r_{t+3} + \dots], \quad (2.2)$$

where  $V_\pi[s_t]$  is the evaluation of the state  $s$  visited at time  $t$ ;  $E_\pi$  is the mean operator with respect to the stochastic behaviour  $\pi$  produced by the actor;  $r_t$  is the reward at time  $t$ ;  $\gamma$  is the 'discount factor' ranging over  $[0, 1]$  (here set at 0.9). Note how the discount factor elevated to increasing powers implies that the farther in time a reward is received, the stronger it is 'discounted' (i.e. multiplied by small numbers).

To see how the evaluator learns to evaluate states on the basis of the rewards obtained in the future, consider the relation existing between the theoretical evaluations  $V_\pi[s_t]$  and  $V_\pi[s_{t+1}]$  of two states visited in sequence, obtained from equation (2.2):

$$V_\pi[s_t] = E_\pi[r_{t+1}] + \gamma \cdot E_\pi \left[ \sum_{k=0}^{\infty} (\gamma^k \cdot r_{t+2+k}) \right],$$

$$V_\pi[s_t] = E_\pi[r_{t+1}] + \gamma \cdot V_\pi[s_{t+1}]. \quad (2.3)$$

As mentioned, the evaluator produces an estimation  $V'_\pi[s_t]$  of the theoretical evaluation  $V_\pi[s_t]$ . On the basis of the evaluator's estimations, equation (2.3) can be approximated as follows:

$$V'_\pi[s_t] \approx r_{t+1} + \gamma \cdot V'_\pi[s_{t+1}]. \quad (2.4)$$

In this approximation, the quantities at the left and right side of the formula are different because the estimations  $V'$  are affected by errors and because  $E_\pi[r_{t+1}]$  has been substituted by the reward  $r_{t+1}$  *actually received at time  $t+1$* . Now note that the two sides of the formula are two estimations of  $V_\pi[s_t]$ , the first *formulated at time  $t$*  and the second *formulated at time  $t+1$* . The key point is that the estimation of the right side,  $r_{t+1} + \gamma \cdot V'_\pi[s_{t+1}]$ , is more accurate than the estimation of the left side,  $V'_\pi[s_t]$ , as it relies upon the actual reward,  $r_t$ , and the estimation  $V'_\pi[s_{t+1}]$  formulated *one step later* with respect to  $V'_\pi[s_t]$ . This suggests that it is possible to improve  $V'_\pi[s_t]$  produced by the evaluator by making it closer to  $r_{t+1} + \gamma \cdot V'_\pi[s_{t+1}]$ . This is the central idea of *time delay learning* (TD learning) proposed by Barto *et al.* (1983), which is also at the core of the functioning of the actor-critic model (see Sutton & Barto 1998). In order to modify  $V'_\pi[s_t]$  in such a way, the weights of the evaluator should be suitably updated. To do so, first the

difference  $S_{t+1}$  between the two mentioned estimations is computed (*surprise* or *TD error*):

$$S_{t+1} = (r_{t+1} + \gamma \cdot V'_\pi[s_{t+1}]) - V'_\pi[s_t], \quad (2.5)$$

and then it is used to update the evaluator's weights with a modified Widrow–Hoff rule (Widrow & Hoff 1960):

$$\Delta w_i = \eta \cdot S_{t+1} \cdot x_i, \quad (2.6)$$

where  $\eta$  is a learning rate (here set at 0.001), and  $x_i$  is the activation of the retina pixels at time  $t$ .

To see how the actor learns to select actions, note how equation (2.6) implies that each evaluator's evaluation tends to become an accurate estimation of the *average* rewards that the system will obtain from the perceived state if the *stochastic* course of action suggested by the actor is followed. For this reason, a positive critic's surprise implies that the action selected by the actor at  $s_t$  has led the system to a new state  $s_{t+1}$  whose evaluation  $V'_\pi[s_{t+1}]$ , integrated with the reward  $r_{t+1}$ , is better than what the critic expected at  $s_t$ , i.e. it is better than the average evaluations of states obtained by the actor in the same state in the past (this also justifies the term 'surprise'). Vice versa, a negative surprise implies that the action selected at  $s_t$  was worse than those selected in the past in the same state. This suggests that the surprise signal can also be used to allow the actor to learn to select actions. More specifically, this can be done as follows: when surprise is positive, the centres of the Gaussians used to randomly draw the actions (these centres can be thought of as a sort of 'average action' associated with  $s_t$ ) are made closer to the actually drawn values (i.e. to the actually executed action), while in the case that surprise is negative, the centres are 'moved away' from them. In mathematical terms, this result can be obtained by updating the actor's weights with a modified Widrow–Hoff rule:

$$\Delta w_{ij} = \zeta \cdot S_{t+1} \cdot (y_j - \mu_j) \cdot (y_j \cdot (1 - y_j)) \cdot x_i, \quad (2.7)$$

where  $(y_j \cdot (1 - y_j))$  is the derivative, with respect to the action potential, of the actor's *sigmoid* output units' activation,  $\zeta$  is a learning rate (here set at 0.02);  $(y_j - \mu_j)$  is the part of the formula that moves the centres of the Gaussians towards (if  $S_{t+1} > 0$ ) or away from (if  $S_{t+1} < 0$ ) the action selected by the actor. Note that, with the exception of  $S_{t+1}$ , all quantities of the formula are computed at time  $t$ .

### 3. RESULTS

#### (a) The basic experiment in square arenas: attraction and repulsion factors (absolute distance)

The first simulated experiment aimed to reproduce the data collected with real chicks trained and tested in square arenas. For this purpose, a simulated chick was first trained to reach the centre of the 70 cm square arena for 500 000 steps. During this training phase, when the chick reached the centre it received a reward of unity and was then randomly repositioned in the arena.

The results indicate that during the training phase the chick very rapidly learns to reach the centre of the arena. In particular, [figure 2](#) shows that after about 100 000 cycles the chick reaches the maximum level of performance (about 0.125) measured as the moving average of the rewards obtained in 5000 cycles (this value means that the chick receives a reward in 12.5% of steps on average, i.e. it finds the food about once every eight steps by following a quite straight path; see [figure 3](#)).

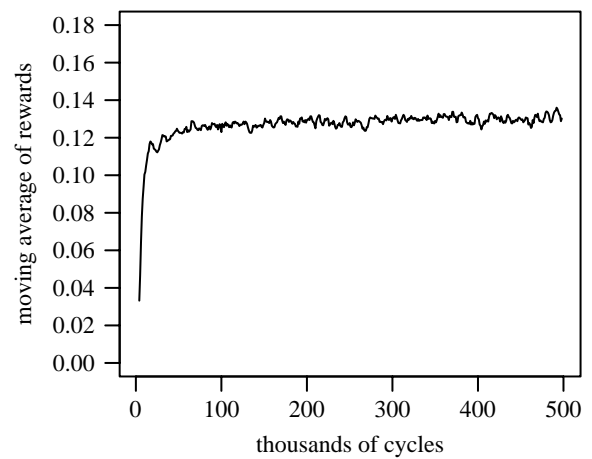


Figure 2. Chick's learning curve corresponding to 500 000 training cycles (x-axis) run in a 70 cm square arena. The performance is measured as a moving average of the number of rewards obtained by the chick in 5000 cycles (y-axis).

The tests in the 70 and 140 cm arenas were carried out as follows. The chick was first set at a random position in the arena and then was left free to explore it for 480 steps (assuming that one step lasts half second, this test lasts 4 min, equal to the duration of the tests run by [Tommasi et al. 1997](#)). This test was repeated 16 times with different seeds of the random number generator to mimic the tests run with different real chicks by [Tommasi et al. \(1997\)](#) (with the difference that here 16 chicks were used, instead of the eight used by [Tommasi et al.](#), to have more reliable data). During these tests, the  $(x, y)$  coordinates of the points visited by the chicks in the arenas were recorded at each step.

The analysis of the density of the points visited during the test in the small arena, shown in [figure 4a](#) and [b](#), indicates that chicks succeed in learning to localize the centre as done by real chicks ([figure 4c](#)). However, in the test in the large arena, chicks explore areas at a distance from walls similar to the distance experienced at the centre of the small arena during learning ([figure 4d,e](#)), as done by real chicks ([figure 4f](#)), but they fail to explore the centre as the latter do. Moreover, the simulated chicks seem to explore more intensely four 'attracting areas' at which two of the four walls have the same appearance as the walls seen from the centre of the small arena. Real chicks did not exhibit this behaviour (cf. [Tommasi & Vallortigara 2000](#)): likely in real experiments this behaviour was hidden by the presence of disturbing uncontrolled variables that were absent in the simulated experiments. Moreover, it is interesting to note that some of the rats tested by [Tommasi & Thinus-Blanc \(2004\)](#) had a behaviour similar to the one exhibited by the model (see §1).

Before investigating in detail the actor's information processing that is behind this behaviour, it is interesting to consider the evaluations produced by the chicks' evaluator in correspondence to different positions and orientations in the arena. These evaluations are reported in [figure 5](#), which shows that in the small arena chicks assign the highest evaluations to places situated at central positions. Moreover, chicks assign a higher evaluation to a given place when they are oriented towards the centre of the arena than when

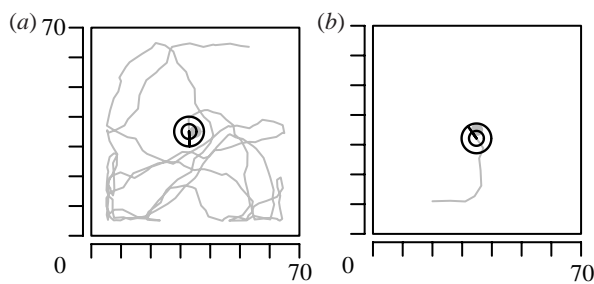


Figure 3. Path followed by a chick in a 70 cm square arena (a) before and (b) after training. The chick is represented with two overlapping circles: the small circle represents the beaking area, while the large one represents its body. The grey circle represents the food target.

they are oriented towards the closer walls: the reason is that in the former condition fewer steps are needed to achieve the target. On the contrary, in the large arena chicks assign the highest evaluations to positions that are at about 35 cm from walls, i.e. the positions where they expect to find the target.

Throughout the paper, the information processing underlying the behaviour exhibited by chicks will be identified by analysing the weights of the actor that connect its input units, corresponding to the retina, to the output unit responsible for the orientation change. Indeed, the configuration of the weights corresponding to the actor's step-size output unit and to the evaluator's evaluation output unit were not very important for understanding chicks' behaviours, so they will not be further discussed in the paper. Given that each of the actor's orientation-unit weights corresponds to a pixel of the retina, it is possible to understand how different images cause the chicks to move in different ways by plotting these weights on a two-dimensional graph and by overlapping on this graph the retina images perceived by the chick when set at different places, and with different orientations, in the arena (cf. figure 1; an example of these weights is shown in figure 6a). When interpreting the effects that different orientation-unit weights have on chicks' behaviour, it is important to keep in mind that: (i) given the way the activation of the orientation-change output unit is mapped onto the actual chicks' orientation change (see §2), *positive weights* (reported in white in the graphs) and *negative weights* (reported in black) tend to cause the chicks to turn, respectively, left and right and (ii) for reasons that will be clarified below, in all experiments the weights of the maps tend to organize in *five bands along the vertical dimension* (in the graphs these bands will be identified by five black vertical segments) and *two halves* along the horizontal dimension in which weights that occupy specular positions have same absolute values and opposite signs (see figure 6a for an example).

Figure 6 shows the map of the orientation-unit weights of the chick trained in the 70 cm square arena with three different retina images overlapped on it. The figure shows that, on the left half of the map and from top to bottom, the five bands of weights are, respectively, negative, positive, (close to) null, positive and negative. Moreover, as mentioned above, the right

half of the map has a specular organization with weights with opposite signs. The figure shows that vertical edges activate the weights of the map as follows: (i) they activate all bands if they are closer than 35 cm to the chick, (ii) they activate the second, third and fourth bands if they have a distance between 35 and 70 cm, and (iii) they activate only the third central band if they are more than 70 cm distant (the weight of the third band is developed only on the basis of vertical edges). Horizontal edges activate the retina units corresponding to the weights of the map as follows: (i) upper and lower edges of walls closer than 35 cm to the chicks, activate the weights of, respectively, the first and fifth band, (ii) upper and lower edges of walls at a distance between 35 and 70 cm activate, respectively, the second and fourth band, and (iii) upper and lower edges of walls at a distance larger than 70 cm activate only the third band (note that this can happen only in the 140 cm arenas).

Vertical edges have negligible effects on chicks' behaviour. In fact, the weights of the third (central) band, activated only by vertical edges in the 70 cm arena and mainly by them in larger arenas, are close to zero (null weights do not affect the chicks' behaviour). Moreover, whenever vertical edges activate the weights of other bands, these weights are also activated by horizontal edges. As the latter activation tends to overwhelm the former one (to see this, compare the number of weights/pixels of these bands activated by vertical and horizontal edges in figure 6a), horizontal edges tend to have effects on chicks' behaviour that overwhelm the effects of vertical ones. This interpretation will be further supported by the experiments illustrated in §3b.

Regarding horizontal edges, figure 6 shows that the weights of the left and right halves of the map have absolute values symmetrical with respect to the vertical line that crosses the centre of the map, but opposing signs. This indicates that the chicks behave in a 'specular' way to stimuli positioned at their left or right side. Let us focus on the left half of the map of weights and on chicks' behaviour in the 70 cm arena. As mentioned, the weights of the first and fifth band correspond to retina units that are activated by, respectively, upper and lower *horizontal edges* of walls positioned *at less than 35 cm* on the left of the chicks: as these weights are negative, they cause the chicks to turn right, i.e. to *move away* from these walls ('repulsion factor'). The weights of the second and fourth band are activated by horizontal edges of walls positioned at a distance *between 35 and 70 cm* on the left of the chicks: as these weights are positive, they cause the chicks to turn left, i.e. to *move towards* these walls ('attraction factor'). The same kind of reasoning holds for the right half of the map of weights activated by horizontal edges of walls positioned at the right side of chicks (the sign of weights is inverted because now the chicks have to turn right to move towards walls and turn left to move away from them). The only conditions in which the chicks move straight are either when they are at the centre of the arena or when they are in any other position in it with an orientation towards the centre of the arena. In fact, in these circumstances the image of the horizontal edges activates symmetrical



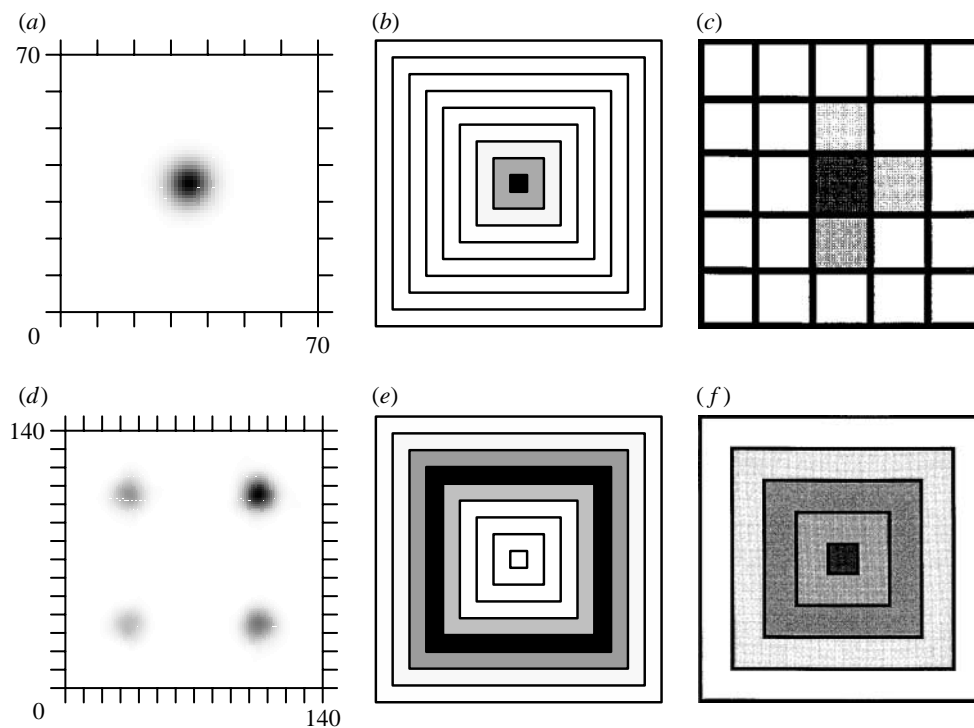


Figure 4. Average density (grey levels) of places visited by 16 chicks, measured in tests lasting 480 cycles each, in the (a) 70 and (d) 140 cm square arenas (the density was computed with a normal kernel smoothing algorithm using  $70 \times 70$  cells and a standard deviation of 10 cells). (b, e) display the same data in a format similar to the one used in the graphs reported in Tommasi *et al.* (1997) for real chicks and shown in (c, f) for comparison (Copyright: *Journal of Comparative Physiology A*, Springer-Verlag).

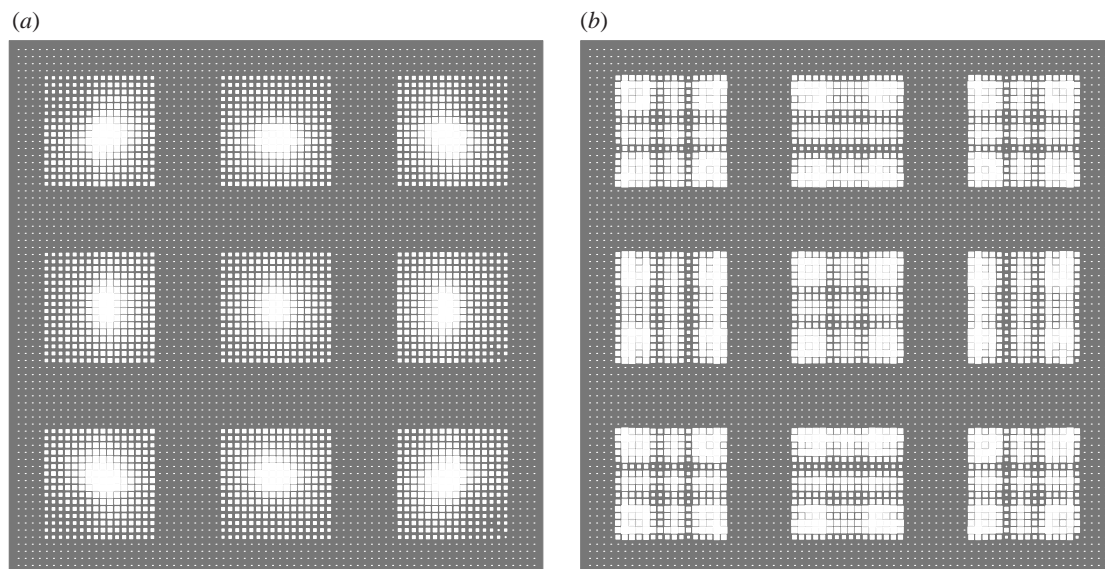


Figure 5. Evaluations that the trained chick associates with different places in the (a) 70 and (b) 140 cm square arenas. Each graph is composed of nine grids; the northwest grid of the eight external grids corresponds to a northwest orientation of the chick, the north grid corresponds to a north orientation of it and so on. The central grid is an average of the external eight grids. Each grid shows the evaluations that the chick associates with  $16 \times 16$  different places in the arena: each evaluation is represented by a white small square having an area proportional to its level. All the evaluations reported in the graphs range over  $[0, 1]$ .

weights of the left and right halves of the map: as these weights have the same absolute value and opposite signs, chicks move straight (note that the condition in which chicks have the target precisely behind them is an unstable-equilibrium condition from which they easily come out by exploiting noise factors). Overall, the effects of these factors are that chicks tend to reach the centre of the 70 cm arena by moving to an absolute distance from walls of about 35 cm.

Figure 6e illustrates why, when tested in the large arena, chicks move to the four 'attractor places' shown in figure 4d. The map of weights shows that horizontal edges of walls more than 70 cm distant from the chicks, i.e. more than half the size of the large arena, activate the weights of the third (central) band of the map of weights and so have little effects on the chicks' behaviour (recall that these weights are close to zero). As a consequence, chicks' behaviour is dominated by walls closer to them



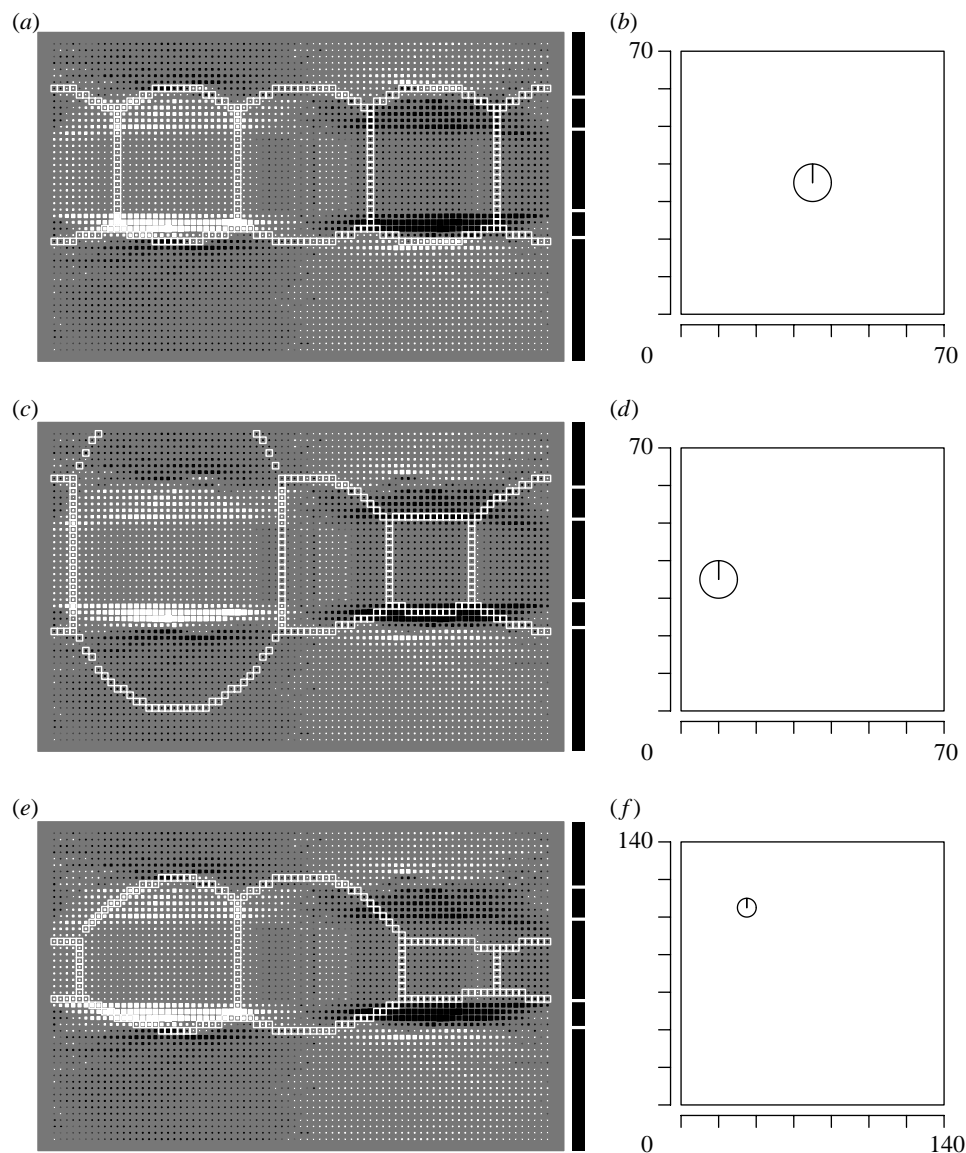


Figure 6. (a, c, e) show the map of weights of connections between the retina's units to the actor's orientation-change output unit in the chick trained in the 70 cm square arena. White and black squares correspond, respectively, to positive and negative weights; when activated these cause the chicks to turn left and right, respectively. The areas of squares are proportional to the absolute values of the corresponding weights. The black vertical segments on the right of the three graphs indicate the five bands of weights to which the text refers. The squares highlighted with white borders in the three graphs indicate retina images perceived by chicks at the specific positions in the arenas and with the specific orientations shown by the three corresponding graphs (b, d, f) (these graphs show arenas that measure 70, 70 and 140 cm, respectively).

than 70 cm: this implies that only two of the four walls for the arena affect chicks' behaviour. These walls tend to 'repel' or 'attract' chicks, until they are 35 cm distant from them, on the basis of the same factors operating in the 70 cm arena described above.

#### (b) *The effects of horizontal edges in circular and square arenas: the absolute distance factor*

In order to confirm the interpretations of the effects of horizontal edges on chicks' behaviour, a second and third set of experiments were carried out using, respectively, square and circular arenas with chicks that could perceive only horizontal edges. Carrying out the experiments with circular arenas was important for two reasons: (i) these experiments allowed isolation of the effects of horizontal edges by eliminating all information about distances of walls present in square arenas, provided by both vertical edges and the undulation

of horizontal edges, and (ii) the results obtained with circular arenas could be compared with the results obtained with real chicks in these arenas (cf. §1).

In the first set of experiments, a simulated chick capable of perceiving only horizontal edges was first trained in the 70 cm square arena, with the same modalities as those used in the experiments illustrated in §3a, and then it was tested 16 times, with different random number generator's seeds, both in the same arena and in the 140 cm square arena. An analogous set of experiments was conducted with circular arenas.

The results of the test phase of both sets of experiments show that in the small arenas chicks search for food at central areas, while in the large arenas they search at areas that have a distance of about 35 cm from walls. Remarkably, the results obtained in the tests conducted with circular arenas closely match those exhibited by real chicks, as shown in figure 7.

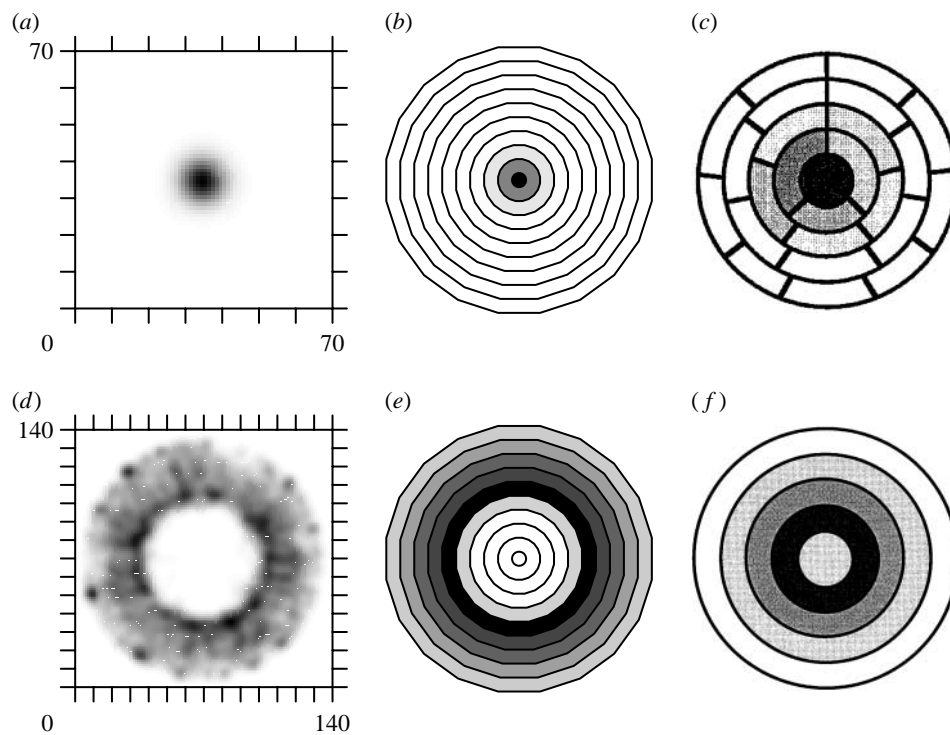


Figure 7. Average density (grey levels) of places visited by 16 chicks, measured in tests lasting 480 cycles each, in the tests in the (a) 70 and (d) 140 cm circular arenas. (b, e) display the same data in a format similar to the one used in the graphs reported in Tommasi *et al.* (1997) for real chicks and shown in (c, f) for comparison (Copyright: *Journal of Comparative Physiology A*, Springer-Verlag).

Figure 8*a,b* show the maps of the weights relative to the actor's orientation-change output unit of the chicks trained, respectively, in the 70 cm square and circular arenas. These maps are very similar to each other and to the map obtained with the square arena and vision of both horizontal and vertical edges (cf. figure 6). The main difference relates to the third (central) band of the maps: in the two novel conditions this band has zero weight, while in the previous condition it had weight close, but different, to zero. This confirms that in the previous condition, and as suggested in §3*a*, these weights were updated on the basis of vertical edges. Moreover, the fact that the behaviour of chicks with and without the perception of vertical edges is identical in the square arenas confirms that these weights have little effects on chicks' behaviour, as again suggested in §3*a*. Finally, the fact that the weights of the other four bands of the map of the two new conditions are very similar to those of the previous condition, implies that the explanation of chicks' behaviour is the same as that presented in §3*a*: chicks tend to move away from or towards the walls in order to be at a distance from them similar to the distance from walls experienced at the centre of the training arenas, i.e. approximately 35 cm.

#### (c) The effects of vertical edges and surfaces in square arenas: the repulsion factor

In order to isolate the effects of vertical edges on chicks' behaviour, the training and test experiments with square arenas were repeated with chicks that perceived only vertical edges. A first interesting result obtained is that the learning process is now much slower with respect to previous experiments, even if it is still ultimately successful (cf. figures 9 and 2). This indicates that chicks have more difficulties in learning

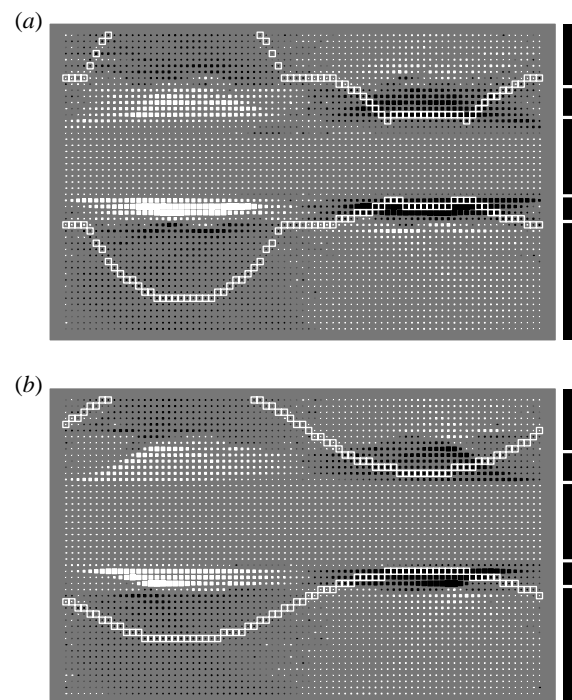


Figure 8. The map of weights relative to the actor's orientation-change output unit of a chick that could see only horizontal edges and was trained (a) in a 70 cm square arena and the analogous weights of a chick trained (b) in a 70 cm circular arena. The black vertical lines on the right of the graphs indicated the five bands of weights to which the text refers. The images overlapped to the maps correspond to a position and orientation of the chick in the two arenas similar to those shown in figure 6*d*.

to navigate on the basis of vertical edges compared to horizontal ones. This is also in line with what was noticed in §3*a*: when chicks perceive both vertical and

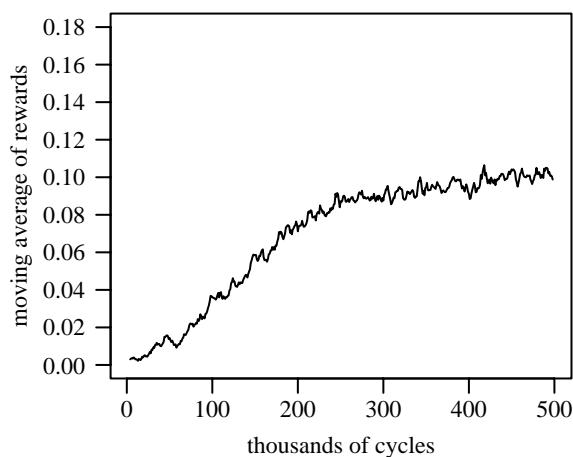


Figure 9. Learning curve of a chick that perceives only vertical edges, corresponding to 500 000 training cycles ( $x$ -axis) in a 70 cm square arena. The performance is measured as the moving average of the number of rewards obtained by the chick in 5000 cycles ( $y$ -axis).

horizontal edges, the latter tend to dominate their behaviour. This might be caused by the fact that when chicks perceive both types of edges, the learning process focuses on the more easily exploitable source of information.

The results of the tests carried out in the 70 cm arena show that chicks explore the centre of it, while the results of the tests in the 140 cm arena show that chicks wander in the whole area of the arena corresponding to places with a distance larger than 35 cm from any wall (figure 10).

Figure 11*a*, which shows the map of weights corresponding to the actor's orientation-change output unit, allows explanation as to why chicks exhibit these behaviours. During training, the actor mainly develops the weights that correspond to a behaviour of repulsion from walls (first and fifth band of the map, plus a large portion of the second and fourth): these weights are generated by the 'tips' of the images of vertical edges of walls closer than about 35 cm to the chicks. During learning these weights assume the same role as that assumed by the corresponding weights in the experiments with horizontal edges illustrated in §3*b*: large vertical images correspond to close corners of the arena from which chicks *move away*. The weights of the third band of the map are now wholly positive and negative, respectively, in the left and right half of the map. These weights tend to lead chicks towards the centre of the arena, as will be shown in detail in §3*d*: Likely, these two effects tend to sum, so chicks tend to explore places of the whole central area of the 140 cm arena more than 35 cm distant from all walls (figure 10).

Interestingly, similar results were obtained when the 70 cm square arena was used to train and test chicks that perceived the whole *walls' surface* (see the image overlapping the map of weights reported in figure 11*b*). In these experiments, the units of the retina that corresponded to the whole surface of walls were activated with 0.05 (activations close to unity, as those used for edges caused instability in the learning process due to the large number of pixels activated by walls' surfaces). In the test in the 140 cm arena, chicks exhibit a behaviour that is very similar to that

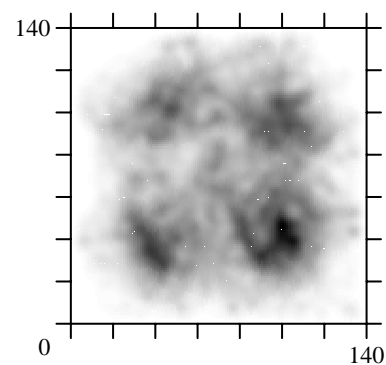


Figure 10. Density (grey levels) of places visited by 16 chicks in tests that lasted 480 cycles each and were carried out in the 140 cm square arena. The chicks perceived only vertical edges and had been trained in a 70 cm square arena.

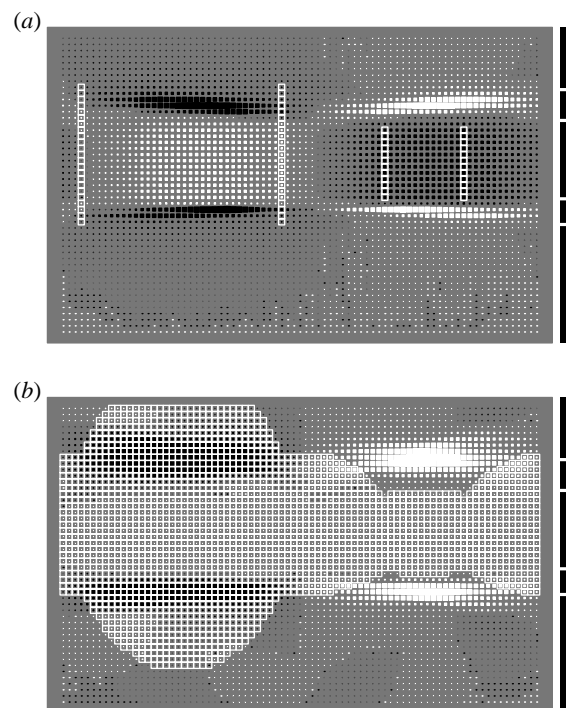


Figure 11. The map of weights relative to the actor's orientation-change output unit of a chick that could see only (*a*) walls' vertical edges or (*b*) walls' surfaces and had been trained in a 70 cm square arena. The black vertical segments on the right of the graphs indicate the five bands of weights to which the text refers. The images overlapping the maps correspond to a position and orientation of the chick similar to those shown in figure 6*d*.

illustrated in figure 10 (data not reported): they are repelled by walls closer than 35 cm and wander in the whole central area of the arena. Indeed, the map of weights reported in figure 11*b* shows that the weights of the third band, and those of half of the second and fourth, are null. This is due to the fact that these weights are always activated by walls' surfaces, independently of the walls' distance: this causes them to sum positive and negative adjustments with a total null effect. As a consequence, walls farther than about 35 cm have no effect on chicks' behaviour. Moreover, the first and fifth bands are very similar to those of the experiments with vertical edges. This implies that the upper and lower part of the walls play a role similar to



that played by the tips of vertical edges seen above: chicks move away from walls closer than 35 cm.

**(d) Other effects of vertical edges in square arenas: the relative position factor**

The experiments presented so far failed to reproduce the behaviour of real chicks that generalized their ability to find the centre of square arenas with doubled size. However, the results of the first simulation presented in §3c, relative to chicks that could perceive only vertical edges in a square arena, showed that even if their behaviour was dominated by the walls' repulsion factor based on the vertical edges' tips, the *invariant central part* of these edges generated an interesting configuration of the corresponding weights of the actor's orientation-change output unit (third band of the map of figure 11a). Could these weights tend to produce the generalizing behaviour of chicks? A first theoretical analysis suggests that the answer to this question is affirmative. As those weights correspond to the portions of vertical edges invariant with respect to distance, the image of a *single edge* that activates them cannot provide information useful for navigation to chicks. This suggests that if those portions of vertical edges carry information useful for navigation, this information has to be based on their relative position along the horizontal axis of the retina, i.e. on the horizontal plane of the environment. More specifically, as vertical edges are not distinguishable from each other, that information has to be related to their *relative density in space*. Indeed, vertical edges that are denser in a portion of the perceived space are farther from the chicks than vertical edges that appear sparser. The map of weights illustrated in figure 11a suggests that this interpretation is correct. In fact, the weights of the third band of the map are positive and negative in correspondence to, respectively, the left and right halves of the retina. As a consequence, if vertical edges appear denser in the left half of the retina, chicks tend to turn right, while if edges appear denser in the right half of the retina, chicks tend to turn left.

To support this interpretation, the experiments with square arenas were repeated with chicks imagined to *focus their attention* on the invariant part of the vertical edges. In order to accomplish this, each vertical edge was represented on the retina as a vertical segment that covered the whole retina's height (see the image overlapping the map of weights in figure 12). This assumption might appear arbitrary at first sight: on the contrary, §5 will show that it is theoretically sound and relevant. Moreover, note that in these simulations, the input layer of the controller of chicks should be interpreted as an *internal representation* resulting from a pre-processing of the image of the environment, rather than as a retina image.

A first relevant result of the experiments carried out with this chick is that the learning curve of the training phase is similar to that shown in figure 9 (data not shown). This confirms that the use of vertical edges for navigation is more difficult than the use of horizontal ones. This is likely due to the fact that chicks exploit the horizontal edges of single walls to move to specific distances from one or more of them, while they exploit the information carried by vertical edges by comparing

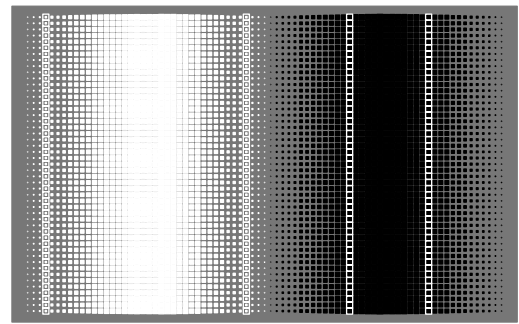


Figure 12. The map of weights relative to the actor's orientation-change output unit of a chick that focused attention on the position of vertical edges on the horizontal plane and was trained in a 70 cm square arena. The image overlapping the map corresponds to a position and orientation of the chick in the arena similar to those shown in figure 6d.

their relative positions, as mentioned above: the latter capacity takes more time to be learned than the former.

A first interesting result regarding the behaviour that chicks exhibit in the testing phase is that they not only search at the centre of the 70 cm arena, but they also generalize this capability to the 140 cm arena (the graphs of the density of search in the two arenas, not reported for brevity, are similar to figure 4a). Another result is that the interpretation provided at the beginning of this section about the weights of the actor's orientation-change output unit, relative to the portions of the vertical edges perceived as invariant, is confirmed by the map of weights emanating from the new experiment (see figure 12). These weights have signs and absolute values similar to those of the central band of the map emanating from the experiments with vertical edges (see figure 11a). This implies that the strategy of navigation employed by chicks consists of moving towards the region of space where there appears to be a relatively higher density of vertical edges, as this density correlates with the distance of the corners of the arenas.

**(e) Correlations between the maps of weights**

It is now possible to present the correlations between all the maps of weights generated by the experiments presented so far (see figure 13). Computing these correlations allows us to corroborate or refute the interpretations of the experiments presented in the previous sections because positive correlations between two maps of weights indicate that the relative navigation tasks are tackled by chicks on the basis of the same navigation strategy, while negative correlations suggest that the opposite holds.

The simulated experiments presented in §3a–d can be grouped in three classes on the basis of the main factors that explain chicks' behaviours in the various conditions: (i) 'horizontal and vertical edges and square arenas', 'horizontal edges and square arenas', 'horizontal edges and circular arenas': in these three conditions chicks' behaviour is mainly explained by the walls' attraction and repulsion factors, based on the absolute distances from walls estimated on the basis of the perceived height of horizontal edges, (ii) 'vertical edges and square arenas', 'walls' surfaces and square arenas': in these two conditions chicks' behaviour is



	1.00					
	<b>0.93</b>	1.00				
	<b>0.46</b>	<b>0.47</b>	1.00			
	-0.23	-0.42	-0.09	1.00		
	-0.21	-0.27	0.30	<b>0.41</b>	1.00	
	<b>0.75</b>	0.20	0.00	<b>0.96</b>	0.05	1.00

Figure 13. Correlations ( $R^2$ ) between the actor's maps of weights presented in the previous sections. The little pictures at the left of the rows and below the columns of the table sketch the relative experiments in terms of the images perceived by chicks (from top to bottom beside the rows: 'horizontal and vertical edges in square arenas'; 'horizontal edges in square arenas'; 'horizontal edges in circular arenas'; 'vertical edges in square arenas'; 'walls' surfaces in square arenas' and 'position of vertical edges in square arenas'). Bold and grey text aid the identification of high and low correlations, respectively (considered as such when above and below 0.35, respectively).

mainly explained by the walls' repulsion factor, based on the perceived height of vertical edges and walls' surfaces, and (iii) 'invariant parts of vertical edges and square arenas (two experiments with vertical edges of §§3a,c)', 'position of vertical edges in space and square arenas': in these three conditions chicks' behaviour is mainly explained by the tendency to move towards the centre of arenas, based on the relative position (density) of landmarks on the horizontal plane, i.e. on the equalization of distances between vertical edges (walls' width).

Figure 13 reports the correlations of the maps obtained in all these conditions (note that the correlations between the map produced by the experiment carried out with chicks focused on the position of vertical edges in space—shown in figure 12—and the other maps were computed only with respect to the weights of the central bands: this was done to support or disprove the hypothesis on attention and the 'relative position factor'). The figure shows low correlations between experiments belonging to different classes and high correlations between experiments belonging to the same class (the high range of the correlation coefficients within the same class, for example 0.93 versus 0.46 and 0.47 in class (i), is due to the differences between the images projected by the walls of square and circular arenas). These results corroborate the interpretations presented in §3a–d relative to the specific factors that underlie the behaviours that chicks exhibit in the experiments belonging to each one of the three classes.

#### (f) *The absolute distance and relative position factors: the selective attention hypothesis*

The results reported in §3a–d have not yet explained the behaviour exhibited by real chicks in the test with the 140 cm square arena (i.e. the exploration of both the areas at the centre of the arena and at about 35 cm

from walls). However, they suggest that such behaviour might be based on two types of information: horizontal edges and position of vertical edges in space. Also the experiments of Tommasi & Vallortigara (2001) support the idea that two 'factors' underlie such behaviour (see §1). To verify the computational plausibility of this hypothesis, the experiments with the square arenas were replicated using simulated chicks endowed with two 'retinas': the first retina encoded horizontal edges and the second retina encoded the position of vertical edges in space (as in §3d, these should be thought of as internal representations of percepts rather than actual retinas).

The results of the test carried out in the 140 cm arena after the training phase contradict expectations. First, they show that it is necessary to weight the effects that the two retinas produce on chicks' behaviour, otherwise horizontal edges dominate it and chicks explore only places at about 35 cm from walls. In order to find the suitable weights to balance the effects of the two retinas on behaviour, the training phase was run several times, each time by constantly multiplying the activation of the horizontal-edge retina's units by a different number smaller than unity (while the activation of the vertical-edge position retina's units was, as usual, zero or unity). The result of this search indicated that the balance between the two factors can be achieved with a value of 0.26 (see figure 14). Note that an iterative process was used to find this number as it seemed too difficult to compute it in a direct fashion, for example analytically. In fact, the areas visited by the chicks depended on the complex circular dynamic interplay between their turning/translating movements and the resulting percepts (i.e. the activations of the two retinas).

Moreover, and unexpectedly, the results of the simulation with a weight of 0.26 show that, even balancing the two factors, chicks uniformly explore the areas of the arena that are farther than about 35 cm from walls (see figure 14b). This indicates that chicks tend to exhibit a behaviour that is a mixture of the behaviours generated by the two factors operating separately.

These results suggest a different hypothesis to explain the behaviour of real chicks, again involving attention: while searching for food in the arenas, real chicks do not use the two factors synchronously, but one factor at a time on the basis of a *selective attention process*. In particular, when chicks focus their attention on the position of vertical edges in space, they search at the centre of the arena, while when they focus on horizontal edges they search at about 35 cm from walls.

In order to test the computational plausibility of this hypothesis, the experiments with square arenas were repeated with chicks that used only one retina at each step, i.e. they focused attention on only a subset of the environment's features. Moreover, at each step chicks switched the focus of their attention on the other retina with a probability of 1%: this implied that, on average, attention remained on one factor for 100 steps, i.e. 50 s. Note that these features were hard-coded in the algorithms of the model, i.e. they were not the result of a learning process. Also note that the experiment did not simulate the control of the attention process as the attention switches took place randomly, but only the effects of the presence of such process.

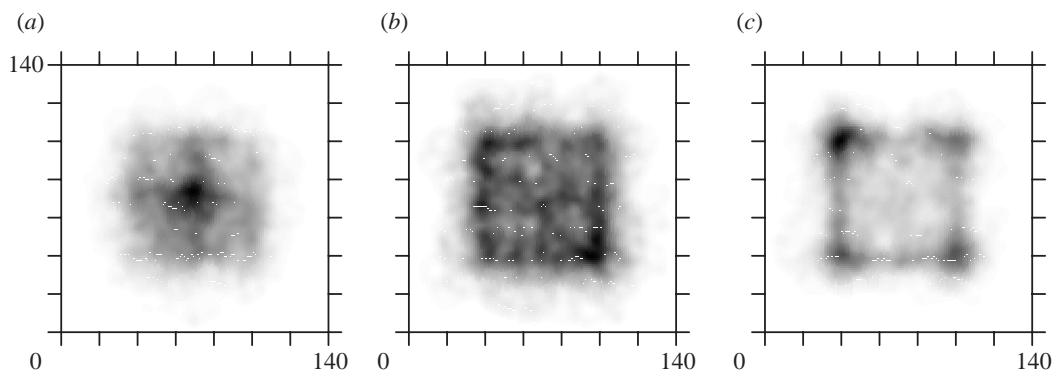


Figure 14. The three graphs show the average density (grey levels) of places visited by 16 chicks in tests that lasted 480 cycles each and were run in the 140 cm square arena under three different conditions. The chicks of these tests, trained in the 70 cm square arena, had two weighted ‘retinas’, one encoding horizontal edges and the other one encoding the position of vertical edges in space. The three conditions differed with respect to the values used to weight the activations of the horizontal-edge retina’s pixels (see text), and are equal to (a) 0.22, (b) 0.26 and (c) 0.30, respectively.

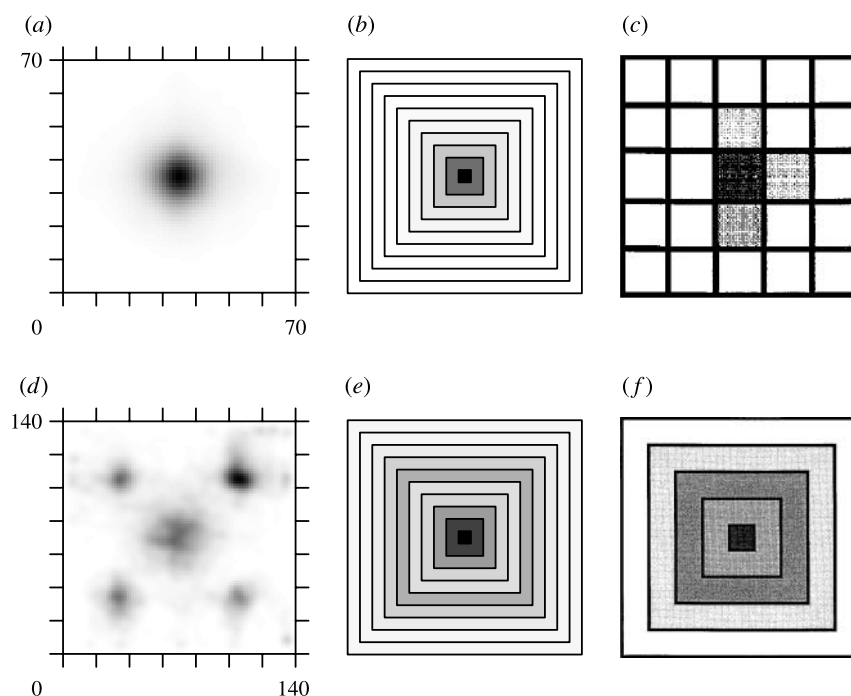


Figure 15. Average density (grey levels) of places visited by 16 chicks, measured in tests lasting 480 cycles each, in the (a) 70 and (d) 140 cm square arenas. (b, e) display the same data in a format similar to the one used in the graphs reported in [Tommasi \*et al.\* \(1997\)](#) for real chicks and shown in (c, f) for comparison (Copyright: *Journal of Comparative Physiology A*, Springer-Verlag).

The results of the test carried out in the 140 cm square arena with chicks trained in the 70 cm square arena, and a balancing weight of 0.26, show that the hypothesis on the attention process is computationally plausible: chicks search the food target both at the centre of the arena and at about 35 cm from walls (see [figure 15](#)), in line with the behaviour exhibited by real chicks (however, note how [figure 15f](#), relative to real chicks tested in the 140 cm square arena, shows that they explore areas at an absolute distance from walls slightly larger than 35 cm: this is likely due to uncontrolled noise factors present in the tests with real chicks, or, alternatively, it reflects some factors underlying real chicks’ behaviour that were not captured by the model).

Before closing this section, it is important to consider how compelling it was to introduce an attention process that focused on only one of the two retinas at a time versus a model that used them synchronously. First, note that during training in the small-square arena, both

retinas developed weights that tended to produce the same behaviour (i.e. ‘move to the centre’). As a consequence, in the test with chicks with no attention process in the large arena, the two retinas tended to produce two different behaviours that mixed in a disruptive additive way (i.e. ‘move to the centre’ and ‘move to areas at 35 cm from walls’). Now, one might wonder: was it possible to design a model that used the two retinas synchronously but developed the capacity to use them in a non-additive way so as to reproduce the behaviours exhibited by real chicks in square arenas? The answer to this question seems negative for two reasons: (i) one possibility to design a non-additive model was to hardwire a non-additive use of the two retinas into it; this solution was discarded since the resulting model would always have used the information from the two retinas in a non-additive way, while it seems plausible that in biological systems the ‘default’ strategy is to attempt to use different available sources of

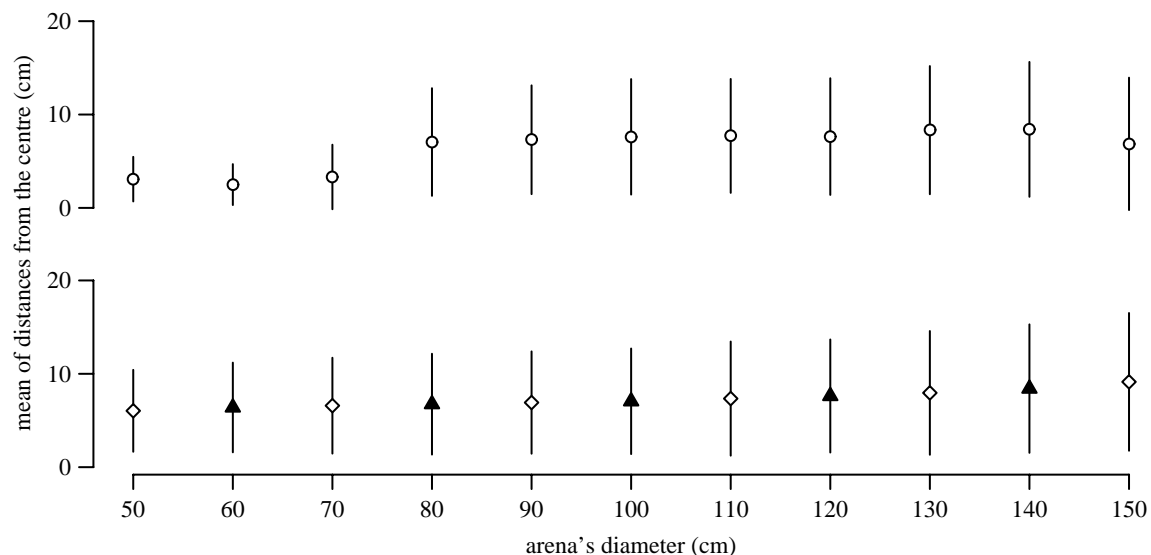


Figure 16. Generalization behaviour in various circular arenas (filled triangles) of chicks trained in circular arenas having different diameters (empty diamonds) and performance in the same arenas of chicks with directly designed weights (empty circles). *X*-axis: diameters of the arenas. *Y*-axis: average distances and standard deviations from the arenas' centres of places visited by chicks.

information in an additive linear fashion as this is easier and faster to do, and (ii) a second possibility was to induce the model to use the two retinas in a more sophisticated fashion through a suitable training phase where the default strategy failed (note that to allow nonlinear behaviours to emerge it would have been necessary to introduce a hidden layer of units in the actor and in the evaluator): this solution was not viable while remaining within the experiments carried out with real chicks (see §4 for an example of an experiment based on this idea). Indeed, at one stage of the research this possibility was considered (e.g. to mimic some tendencies that chicks might have learned phylogenetically), but it was then abandoned since it led to assumptions that were more complicated than the attention hypothesis.

#### 4. AN EMPIRICAL PREDICTION OF THE MODEL

The experiments illustrated in §3 suggest that the model can generate some interesting empirical predictions that can be tested in experiments with real chicks. In particular, the fact that the simulated chicks were capable of learning to find the centre of arenas on the basis of the 'equalization' of the position of vertical edges on the horizontal plane, and the results of the experiments on Clark's nutcrackers reported in Kamil & Jones (1997) (see §1), suggested that, through a suitable training process, it would have been possible to induce the simulated chicks to learn to localize the centre of arenas on the basis of the equalization of the height of walls (i.e. horizontal edges). This prediction was tested in simulation with the following experiment.

A simulated chick that perceived only edges was trained to search for food hidden at the centre of circular arenas having different diameters: 50, 70, 90, 110, 130 and 150 cm—note that these measures are separated by a distance of 20 cm, as in Kamil & Jones (1997). More specifically, these arenas were used in sequence, and were changed each time chicks reached the food, during a training phase that lasted 2 000 000 cycles.

The training phase was followed by a testing phase that led to remarkable results. Chicks not only search at the centre of the various arenas used during training, but they also search at the centre of novel arenas having diameters measuring 60, 80, 100, 120 and 140 cm, so exhibiting generalization capabilities similar to those found in Clark's nutcrackers (see figures 16 and 17). Interestingly, when the same chicks are tested in a square arena with sides measuring 140 cm, they again explore the central area of it so showing that the mechanisms underlying their behaviour are very robust (data not shown).

The map of the weights of the actor that emerged in these experiments (figure 18a) is more complex and hence more difficult to interpret than the maps shown in §3. However, at a first analysis the map seems to confirm that chicks' behaviour is based on the equalization of the perceived *height of walls*. To see this, the map has to be compared with that obtained in the circular arena of 70 cm (see figure 8b). This comparison shows that: (i) the non-zero weights now occupy almost all the central area of the map: this implies that even horizontal edges of far walls now affect chicks' behaviour (contrary to what happened in the other condition; see §3b), (ii) in each of the four quadrants of the map, the gradient of weights changes monotonically, with a certain approximation, from the centre to the top (or from the centre to the bottom; e.g. in the top-left quadrant the weights change progressively from high positive values to high negative values), and (iii) as usual, weights of the two halves tend to have symmetric absolute values with respect to the centre and opposite signs. These properties of the map imply that the only condition where chicks do not turn is when the perceived heights of horizontal edges on the left and right half of the retina equalize. For example, in the condition illustrated in figure 18a, the wall on the left of the chick is closer to it than the wall on its right: this causes the chick to turn

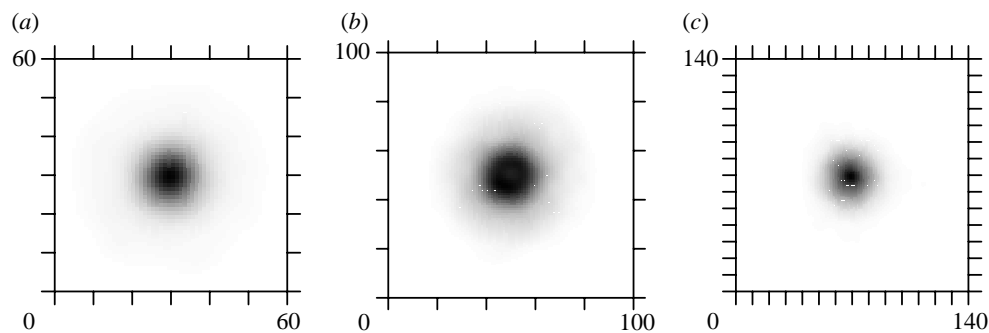


Figure 17. Density of places visited by chicks trained in circular arenas having different diameters, in tests carried out with three novel circular arenas with diameters measuring (a) 60, (b) 100 and (c) 140 cm, respectively.

right (i.e. away from the closer walls) because the image of edges activates relatively more negative weights than positive weights.

To further support this interpretation, a map of the weights of the actor's orientation-change output unit that had the features (i), (ii) and (iii) listed above was directly designed using a Gaussian function that reproduced a gradient similar to the aforementioned one; this map is shown in [figure 18b](#) (in pixels the Gaussian had a mean of 29.3 from the bottom of the retina, a standard deviation of 14.7 and was multiplied by a scaling factor of 37). The weights of the actor's step size unit were all set at 0.0152, the average value of the corresponding weights that emerged in the trained chick. The resulting chick exhibited a behaviour very similar to that of the trained chick in the tests with circular arenas of different diameter (see [figure 16](#)). This result supports the claim that the factors (i), (ii) and (iii) listed above actually capture the core mechanisms underlying the behaviour of the trained chick (the fact that the designed weights had details quite different from the weights that emerged in the trained chick, see [figure 18](#), corroborates this conclusion).

## 5. CRITICAL COMPARISON WITH OTHER MODELS

Many computational and robotic models have been proposed in the literature to investigate the results of experiments carried out with real animals engaged in navigation tasks (for some reviews see [Trullier et al. 1997](#); [Franz & Mallot 2000](#)). This section describes some of these models that targeted some of the experiments presented in §1, and compares them with the model presented here. The goal of this comparison is to show their relative strengths and weaknesses, and to show the potential of the presented model to address the results of experiments similar to those targeted here.

The model presented here, if one does not consider the information encoded by the retinas, is an almost straightforward neural implementation of the actor-critic architecture ([Sutton & Barto 1998](#)). In this respect, a partial novelty is the continuous encoding of actions (see equation 2.1 in §2), quite uncommon in the literature (for other examples see [Gullapalli 1990](#); [Doya 2000](#)). Interestingly, in the experiments presented here, a more standard approach based on a discrete encoding of actions (roughly speaking, the actions used were: 'move left a lot'; 'move left a bit';

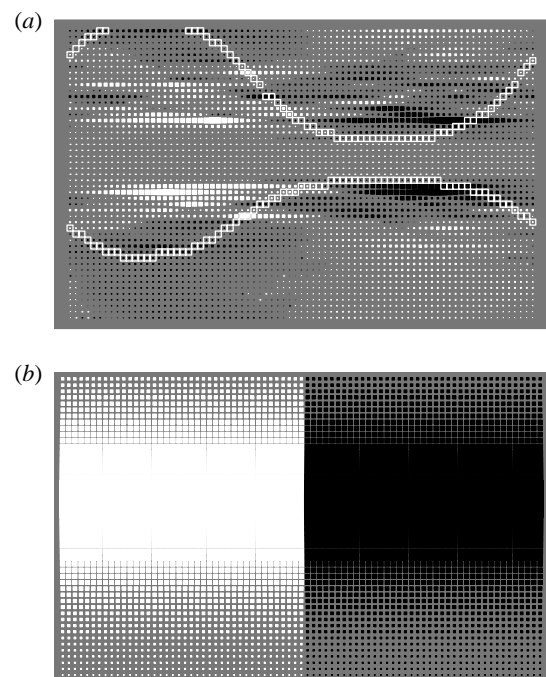


Figure 18. The weights relative to the actor's orientation-change output unit of a chick that was trained in circular arenas of different sizes. (a) The image overlapping the map corresponds to a position and orientation of the chick similar to those shown in [figure 6d](#) in a 140 cm circular arena. (b) Directly designed weights of the actor's orientation-change output unit of a chick that exhibited a behaviour similar to the behaviour produced by the trained chick.

'move straight'; 'move right a bit'; and 'move right a lot') did not allow the chicks to learn to solve the task (this issue was not investigated further because it was beyond the scope of this research).

A first important novelty of the model is the use of the actor-critic architecture together with various types of simulated two-dimensional retinas (or 'internal representations') sensitive to specific features of walls such as vertical and horizontal edges, surfaces, etc. These features were selected on the basis of the processes implemented by vertebrates' visual systems, known to create internal representations that highlight aspects of visual scenes such as objects' borders (see [Hubel \(1988\)](#) for some examples related to cats' visual systems). This, together with the use of very simple (hence easily interpretable) feed-forward networks, was the key to successfully identifying the role played by the different aspects of the environment in chicks' behaviours.



A second important novelty of the model is the introduction of the *attention processes*. A first attention process was introduced in §3*d* to allow chicks to generalize their ability to localize the centre of arenas to arenas with different size, on the basis of the position of vertical edges on the horizontal plane. The successful results obtained on the basis of this assumption suggest that the information on the position of landmarks on the horizontal plane has a general importance for animals' navigation that goes beyond the specific task considered here. If so, it is possible to speculate that evolution developed brains capable of building internal representations focused on such a type of information and endowed them with mechanisms suitable to process it (note that in this case the expression attention process is partially inappropriate because the focusing of cognitive processes would be rigidly set on particular features of the environment). This brings some support to the position illustrated in §1 that holds that some animal species are endowed with dedicated geometrical capabilities.

A second attention process was introduced in §3*f* to successfully reproduce the behaviour exhibited by real chicks in the 140 cm square arena. This aspect of the model is particularly important as it is new with respect to the interpretations provided by the authors of the experiments with real chicks (cf. §1). It would be interesting if experiments carried out with real chicks tried to verify not only the presence and effects of such a process (as done in the simulated experiments shown in §3*f*) but also the mechanisms that control it (in the model the focus of attention was switched by a stochastic mechanism). In this respect, an interesting hypothesis is that real chicks move their focus of attention onto different environmental features when they fail to find the food in the area where they are searching on the basis of the environmental features currently under focus. This hypothesis might also be tested computationally by suitably modifying the model.

Now the model will be compared with other models that addressed specific animal experiments. Miglino & Lund (2001) used a simple feed-forward neural-network model trained with genetic algorithms, and a simulated robot endowed with short-range infrared sensors, to reproduce the behaviour exhibited by rats in the experiments of Cheng (1986) (cf. §1). The model successfully reproduced the behaviours exhibited by control and disoriented rats, and showed that such behaviours could rely on simple sensory apparatuses and clever sensory-motor reactive strategies instead of dedicated geometrical modules and cognitive maps. However, it also had some drawbacks. (i) The acquisition of the capacity to navigate was simulated through a genetic algorithm; these algorithms are suitable for modelling phylogenetic learning but less suitable for modelling the ontogenetic learning usually involved in animals' navigation; for example, in contrast to phylogenetic learning, as ontogenetic learning usually updates subgroups of neural-networks' weights on the basis of information that is 'local' in space and time (e.g. primary reinforcements), it allows systems with a large number of input and hidden units to be studied, such as those required by visual perception that is so important

for animals' navigation. (ii) The robot was endowed with a perceptual apparatus that relied on information that is likely different from that used by real rats (mainly visual). (iii) The sensory-motor strategies developed by the model produced unusual trajectories that are unlikely to reflect animals' behaviours. The model presented here would allow all these drawbacks to be overcome if it were used to reproduce the experiments of Cheng (1986).

Rats' navigation behaviours based on place cells and the functioning of the hippocampus have been widely studied through computational and robotic models. These models can be divided into two classes: (i) models that assume that hippocampus is an auto-associative memory system that creates representations of places that are then associated with actions that lead to the goal, as the model presented here, and (ii) models that assume that the hippocampus is an hetero-associative memory system that creates associations between couples of contiguous places, or of views from them, so as to create a topological representation of the environment (see Franz & Mallot (2000) for more details).

An example of the models of the first class was presented by Burgess *et al.* (1997) (see Recce & Harris (1996) for another example) who studied a robot endowed with vision that had to find a goal place in a square arena similarly to the rats of the experiments presented in O'Keefe & Burgess (1996) (cf. §1). The robot's controller first developed place cells that represented different locations on the basis of estimated distances from walls, and then learned to associate these cells' activation with the direction to the goal. Models similar to this are more suitable than the model presented here to study the development and role played by sophisticated internal representations, like those based on place cells. However, note that it would be easy to add an additional internal layer of units to the actor and/or evaluator of the model presented here (and train them through error-back propagation algorithms—see Rumelhart *et al.* (1986)—instead of a Widrow-Hoff rule as done here): these units might easily develop place cell-like activations, as shown in Treves *et al.* (1992). On the other hand, the model presented here has some advantages with respect to those more sophisticated models because, having a very simple internal structure, it makes it easier: (i) to identify the specific environmental information exploited by animals in particular tasks (e.g. edges, surfaces, etc.; cf. §§3*b,c,d*) and (ii) to compare the relative difficulty with which animals can learn to use different landmarks or features of landmarks for navigation (e.g. horizontal versus vertical edges, cf. figures 2 and 9).

The models of the second class (see Filliat & Meyer (2003) for a review), being quite different from the presented model, are not reviewed in detail here. It is only mentioned that while the models of the first class, being based on place-action associations, allow pursuit of only one goal, the models of the second class, being based on goal-independent topological information on the environment, allow pursuit of many goals (although with the additional cost of the need for suitable *planning processes*; see Franz & Mallot 2000). This implies that the model presented here, that belongs to the

first class, cannot be used to mimic navigation behaviours such as those that require the following of new routes through familiar places (cf. the classic Tolman's problems, e.g. Tolman (1948); but see Foster *et al.* (2000) for a possible interesting way for endowing models like the one presented here with path planning capabilities).

Regarding the experiments that study the errors and generalizations of animals tested in novel conditions, Toombs *et al.* (1998) used a model, based on neural-networks and reinforcement learning, to reproduce the results of the experiments carried out by Collett *et al.* (1986) with gerbils (see §1). The model exhibited behaviours similar to those of gerbils, but it had some limitations that the model presented here would overcome: (i) it used a two-dimensional retina, where the vertical height of landmarks was unrealistically represented with the activation of only one pixel along the vertical dimension: this is prone to introducing distortions in the emergent internal organization of weights of the system (cf. §3c) and (ii) the internal architecture of the model was based on internal modules, each activated by a progressively shifted portion of the retina, which do not have a clear biological correspondent.

Finally, Miglino & Walker (2004) proposed a model to address the experiments that Kamil & Jones (1997) carried out with Clark's nutcrackers (see §1). Remarkably, the model succeeded in reproducing the behaviour of the birds on the basis of a feed-forward evolved neural-network and a simulated robot endowed with a very simple one-dimensional retina. However, in contrast to the model presented here, it did not have the power to explain the role played by the height of landmarks in the birds' behaviour because it was based on a visual system that lacked the vertical dimension (landmarks' height likely played an important role in the experiments of Kamil & Jones (1997) as they did in the experiments targeted here). On the other hand, the model presented here has some features that were decided a priori by the researcher, such as the encoding of the position of vertical edges in space and the selective attention process, which one would have liked to see emerging through learning or evolutionary processes, as would have been possible, at least in principle, by using the artificial life/emergentist approach followed in Miglino & Walker (2004).

## 6. CONCLUSIONS

This paper has presented a neural-network model that allowed the formulation and testing of a specific computationally sound hypothesis on the possible cognitive mechanisms that might underlie some of the behaviours exhibited by domestic chicks while searching for the centre of circular and square arenas. More specifically, the model produced novel results that can be summarized as follows: (i) the model has reproduced, for the first time, the most important behaviours exhibited by real chicks in the experiments of Tommasi *et al.* (1997) and Tommasi & Vallortigara (2000), (ii) the model indicated that the behaviour of searching at specific distances from walls is based on the walls' height as projected on the retina, as hypothesized by

Vallortigara and co-workers, (iii) the model indicated that the generalizing behaviour that leads the chicks to search at the centre of square arenas is based on the equalization of the perceived distances between the walls' vertical edges on the horizontal plane, that is, the walls' width: this explanation is partially new with respect to that proposed by Vallortigara and co-workers, who seemed to suggest an equalization between the perceived heights of walls plus an unspecified role of vertical edges (see §1), (iv) chicks developed the capacity to equalize the width of walls only if they focused part of their cognitive resources on processing the position of vertical edges on the horizontal plane: this interpretation is novel with respect to the interpretations provided by Vallortigara and co-workers using real chicks, (v) the whole behaviour of chicks could be reproduced only by introducing an important assumption regarding the presence of a selective attention process; this process focused chicks' attention on only one typology of landmarks' features at a time, namely on either horizontal edges or on the position of vertical edges in space: also this interpretation is novel, (vi) a novel simulated experiment, not carried out with real chicks, predicted that if chicks were trained in many circular arenas of different size they should develop the capacity to equalize the relative height of walls and should be capable of using it to localize the centre of arenas having novel different sizes and shapes (§4), and (vii) the model has some desirable features, with respect to other similar computational models, that give it the potential to produce sound and unifying interpretations of experiments similar to those targeted here (cf. §5).

The results illustrated also make some contributions to the theoretical issues on cognitive maps debated in the literature on animals' navigation (cf. §1). In particular, the experiments show how simulated chicks tend to encode information that is egocentric and partial (e.g. in the absence of attention processes, they tend to ignore vertical edges when horizontal edges are present). On the other hand, if the assumption of the model relative to the dedicated processing of information on the position of landmarks in space had a correspondent in the cognitive processes of real chicks, it would support the idea that chicks possess a cognitive module specialized in processing geometrical relationships existing between landmarks. This assumption, even without the need to postulate the existence of a dedicated 'geometric module', is not implausible because the relative position of landmarks on the horizontal plane is information fundamental for navigation.

Finally, the model also has the potential to indicate if the differences between the results obtained in experiments employing different animal species are due to different species-specific cognitive processes or to the different experimental designs used. For example, the experiments presented here might provide a possible explanation of the different behaviours exhibited by pigeons and Clark's nutcrackers when engaged in searching for targets located in the middle of an array of landmarks (see §1). Those experiments indicated that while pigeons search at particular distances from specific landmarks when tested with arrays with increased relative distances, Clark's nutcrackers show the generalizing capability of searching at the centre of

such arrays. Sections 3*b* and 4 lead one to interpret the differences of those results as being caused by the different training regimes used, as suggested by Tommasi & Vallortigara (2000), and not in terms of differences between species. In fact the results presented in those sections showed that simulated chicks trained in one specific arena use the height of walls to estimate absolute distances of them and locate targets (§3*b*), while chicks trained in many arenas of different size use the relative height of walls and are capable of using it to localize the centre of novel arenas (§4).

Before closing, it is useful to frame the results presented in the paper in a correct perspective. Some of these results showed that some interpretations of the literature on animals' navigation are sound from a computational perspective while some others are not. However, it is important to stress that simulations can only demonstrate the computational *implausibility* or *sufficiency* of some mechanisms to explain animals' behaviours (or they can suggest novel interpretations), but *not their impossibility or necessity*: these can only be demonstrated by carrying out specific behavioural and neuroscientific experiments with real subjects.

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