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Self-organising thermoregulatory huddling in a model of soft deformable littermates

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Abstract. Thermoregulatory huddling behaviours dominate the early experiences of developing rodents, and constrain the patterns of sensory and motor input that drive neural plasticity. Huddling is a complex emergent group behaviour, thought to provide an early template for the development of adult social systems, and to constrain natural selection on metabolic physiology. However, huddling behaviours are governed by simple rules of interaction between individuals, which can be described in terms of the thermodynamics of heat exchange, and can be easily controlled by manipulation of the environment temperature. Thermoregulatory huddling thus provides an opportunity to investigate the effects of early experience on brain development in a social, developmental, and evolutionary context, through controlled experimentation. This paper demonstrates that thermoregulatory huddling behaviours can self-organise in a simulation of rodent littermates modelled as soft-deformable bodies that exchange heat during contact. The paper presents a novel methodology, based on techniques in computer animation, for simulating the early sensory and motor experiences of the developing rodent.

Keywords: self-organisation; thermoregulation; huddling; shape-matching

Introduction

In cold environments, many species of endotherms keep warm by huddling together. The huddle is a self-organising system, where simple interactions between individuals collectively give rise to group-level emergent properties [1]. Emergent properties of huddling include i) a capacity for thermoregulation amongst the group which exceeds that of the individual [2], ii) a second-order critical phase transition from close aggregation at low environment temperatures to dispersion at high environment temperatures [3], and iii) self-sustaining group dynamics at intermediate temperatures known as 'pup flow', whereby individuals continuously cycle between the warm core and cold periphery of the huddle [4].

Agent-based modelling has helped to establish that these group-level properties can emerge from simple rules of interaction between individuals [5, 6]. Models of huddling have typically studied self-organisation from one of two directions. First, models using simulated or physical robots (even bean bags) have helped establish the importance of the animal morphology in determining how interactions between the body and the environment affect group-level aggregation patterns [7–9]. Second, models based on the thermodynamics of heat exchange have instead described individuals simply as gas particles bouncing around in a chamber [1, 10]. These two levels of description yield complementary insights into self-organisation in the huddle. Additional insight may be gained by constructing an agent-based model of huddling that is constrained by a combination of morphological and thermodynamic factors.

The aim of the current paper is to simulate the thermodynamics of rodent huddling interactions, in groups of agents whose body morphologies deform inside the huddle in a physically plausible way. To simulate soft-body deformation, the model relies on an algorithm called shape-matching, which has found broad applicability in computer animation [11, 12]. The simulation is shown here to recreate the phase transition in huddling as a function of the ambient temperature, as measured experimentally by [3]. The modelling approach could thus be used to generate complex naturalistic patterns of sensory and motor input for models of neural development [13–17], which are expected to vary systematically with the environment temperature as an underlying control parameter.

Methods

A model of self-organising thermoregulatory interactions between rodent littermates is presented. First, a description of the rodent as a three-dimensional soft deformable body is presented, based on the computer animation technique known as meshless deformation by shape-matching [11]. Second, a model of the interactions between individuals that give rise to huddling behaviours, formulated originally for simulations of two-dimensional rat pups [6], is extended to direct the movements of the three-dimensional pups.

Modelling littermates as soft deformable bodies

The arena is defined as a floor with a cylindrical boundary wall of radius $r_{\text{arena}} = 2.0$. Each of $N = 12$ 'pups' is represented as a cloud of points arranged on a sphere of radius $r_{\text{pup}} = 0.25$. Points are spaced (almost) equidistantly on the sphere by a re-mapping after first spacing the points equally on the face a cube with 7^2 points on each of six faces, yielding $n = 294$ points in total.

At each point is a sphere of radius $r_{\text{point}} = 0.05$ and associated with each point is a 3D position vector $\mathbf{p} = [p_x, p_y, p_z]$, a 3D velocity vector $\mathbf{v}$, and a mass m. The locations of the points can be displaced under external forces, e.g., gravity, and by contact of the sphere with a boundary wall or with a sphere belonging to another pup.

The pup is simulated as a soft-deformable body using the shape-matching algorithm of [11]. Essentially, the algorithm minimizes the discrepancy between the current point cloud (after displacement of the points caused by contacts and/or external forces) and the original point cloud (i.e., a spherical arrangement) by gradient descent. Thus, at each timestep the shape-matching algorithm works against the deformation of the body caused by contacts to restore the pup to its original shape.

For full details of the shape-matching algorithm the interested reader is referred to [11], and a brief overview is provided here. The idea is to specify on each iteration a goal position for each point in the point cloud, and to move the points in the direction towards these goal positions. Goal positions are chosen to minimize the discrepancy between the shape defined by the initial arrangement of the point cloud, $\mathbf{x}^0 = [\mathbf{p}_1, \mathbf{p}_2, \ldots, \mathbf{p}_n]$, and that defined by the current positions of the points $\mathbf{x}$. Specifying the goal positions involves finding the rotation matrix $\mathbf{R}$ which minimizes the following expression:

$$\sum_i m_i(\mathbf{R}(\mathbf{x}_i^0 - \mathbf{t}_0) + \mathbf{t} - \mathbf{x}_i)^2,$$

where $\mathbf{t}_0$ and $\mathbf{t}$ are translation vectors. The appropriate rotation matrix can be defined as,

$$\mathbf{R} = \mathbf{A}(\sqrt{\mathbf{A}^{\mathrm{T}}\mathbf{A}})^{-1},$$

where $\mathbf{A} = \sum_i m_i(\mathbf{x}_i - \mathbf{x}_{\mathrm{cm}})(\mathbf{x}_i^0 - \mathbf{x}_{\mathrm{cm}}^0)^{\mathrm{T}}$, and where $\mathbf{t}_0 = \mathbf{x}_{\mathrm{cm}}^0$ and $\mathbf{t} = \mathbf{x}_{\mathrm{cm}}$ are shown by [11] to be the centre of mass of the initial point cloud and the current point cloud, respectively. Then, goal positions are determined by

$$\mathbf{g}_i = \mathbf{R}(\mathbf{x}_i^0 - \mathbf{x}_{\mathrm{cm}}^0) + \mathbf{x}_{\mathrm{cm}}.$$

A vector of external forces $\mathbf{f}_{\mathrm{ext}}$ can be applied to the point cloud on each iteration, and the effects of gravity can be simulated by applying a constant external force in the $-z$–direction; here $\mathbf{f}_{\mathrm{ext}} = [f_x, f_y, f_z - 10]$.

After timestep h, the points are moved towards their goal locations, under the influence of the external force, by

$$\mathbf{x}_i(t+h) = \mathbf{x}_i(t) + h\left(\mathbf{v}_i(t) + \alpha\frac{\mathbf{g}_i(t) - \mathbf{x}_i(t)}{h} + h\frac{\mathbf{f}_{\mathrm{ext}}(t)}{m_i}\right),$$

and velocities are updated as $\mathbf{v}_i(t+h) = h(\mathbf{x}_i(t+h) - \mathbf{x}_i(t))$.

The parameter $\alpha \in \{0, 1\}$ corresponds to the stiffness of the body. Setting $\alpha = 1$ defines a rigid body, and setting $\alpha < 1$ allows the body to deform. Linear deformations, i.e., shear and stretch, can be controlled by an additional parameter $\beta \in \{0, 1\}$, which determines the extent to which goal positions are defined in terms of the optimal rotation matrix $\mathbf{R}$, or the optimal linear transformation $\mathbf{B} = \mathbf{A}\sum_i m_i(\mathbf{x}_i^0 - \mathbf{x}_{\mathrm{cm}}^0)(\mathbf{x}_i^0 - \mathbf{x}_{\mathrm{cm}}^0)^{\mathrm{T}}$, and as such the modified term $\beta\mathbf{B} + (1-\beta)\mathbf{R}$ replaces $\mathbf{R}$ in the computation of the goal locations, $\mathbf{g}_i$.

The algorithm can be further extended to allow for non-linear deformations of the body, i.e., twisting and bending, by redefinition of the matrices $\mathbf{B}$ and $\mathbf{R}$ to include quadratic terms (see [11]). The soft-deformable body of the pup was simulated using this quadratic extension, representing the assumption that pup bodies can bend and twist inside the huddle. A deformation coefficient of

$\beta = 0.5$, a rigidity constant of $\alpha = 0.7$, and a simulation timestep of $h = 0.01$ were used.

At the beginning of a simulation, the initial location of each pup at time $t = 0$ is set to be the center of the arena plus a random displacement in the xy–plane, and each pup, j, is dropped into the arena from a unique height, $\mathbf{x}^0_{\mathrm{cm}} = [r_x, r_y, j]$, where $r_x \in \{-0.25, +0.25\}$ and $r_y \in \{-0.25, +0.25\}$. This ensures that after a few timesteps, all pups will have dropped to the floor (under gravity) to form an initial cluster at the center of the arena.

When the sphere in the point cloud comes into contact with the arena floor ($p_z - r_{\mathrm{point}} < 0$) the corresponding velocity vector is set in the positive z direction and the point is displaced such that $p_z = r_{\mathrm{point}}$. When the sphere comes into contact with the arena boundary ($(|p_x| + r_{\mathrm{point}})^2 + (|p_y| + r_{\mathrm{point}})^2 > r_{\mathrm{arena}}{}^2$), the velocity is averaged with a vector pointing normal to the orientation of the boundary wall ($v_{\mathrm{wall}} = [-\cos\phi, -\sin\phi, 0]$, for $\phi = \mathrm{arctan2}(p_y, p_x)$), and the corresponding position vector is displaced in this new direction.

If the sphere at a point belonging to pup j comes into contact with that at a point belonging to pup $k \neq j$, i.e., $||\mathbf{p}_{j,i} - \mathbf{p}_{k,i}|| < 2r_{\mathrm{point}}$, and the point of pup j is above that of k, the velocity of the point belonging to pup j is set to $\mathbf{v}_{j,i} = \mathbf{p}_{k,i} - \mathbf{p}_{j,i}$ and its position is set to $\mathbf{p}_{j,i} = \mathbf{p}_{j,i} + (\mathbf{p}_{j,i} - \mathbf{p}_{k,i})(2r_{\mathrm{point}} - ||\mathbf{p}_{j,i} - \mathbf{p}_{k,i}||)$. This assymmetry in collision detection/resolution reduces an anomaly that continuously maintained contacts can otherwise cause a pair of pups to 'float' as if unaffected by gravity.

Once any collisions with the arena boundaries and collisions between pups have been resolved, and the affected points have been displaced accordingly, the dynamics of the shape-matching algorithm are applied.

Thermoregulatory huddling behaviours

At this point we have described a method for simulating how a pile of soft bodies can be dropped into a simple arena, how they will deform upon contact with one another, and how they will subsequently come to rest either by stacking atop oneanother or by rolling across the arena floor. However, to actively form and maintain a huddle, movements of the bodies must be self-directed. Here we first describe the dynamics of thermal exchange with the environment and between bodies that are in contact, before showing how 'homeothermotaxic' [6] behaviours of the individuals can direct pups that are in contact towards or away from oneanother, giving rise to self-organising thermoregulatory huddling.

The ambient temperature of the arena is T_a, which is constant for the duration of the simulation. Each pup maintains a dynamic body temperature T_b, and has a preferred temperature $T_p = 0.6$, which is used to represent a desired body temperature, e.g., 37°C. The sphere located at each point in the cloud used to define the pup is now considered to be a thermal-tactile 'afferent'. By default, each afferent measures the ambient temperature T_a. However, if the afferent is in contact with the afferent of another pup, T_c is set to the current value of T_b of the other pup.

According to the huddling model of [6], the body temperature is updated by

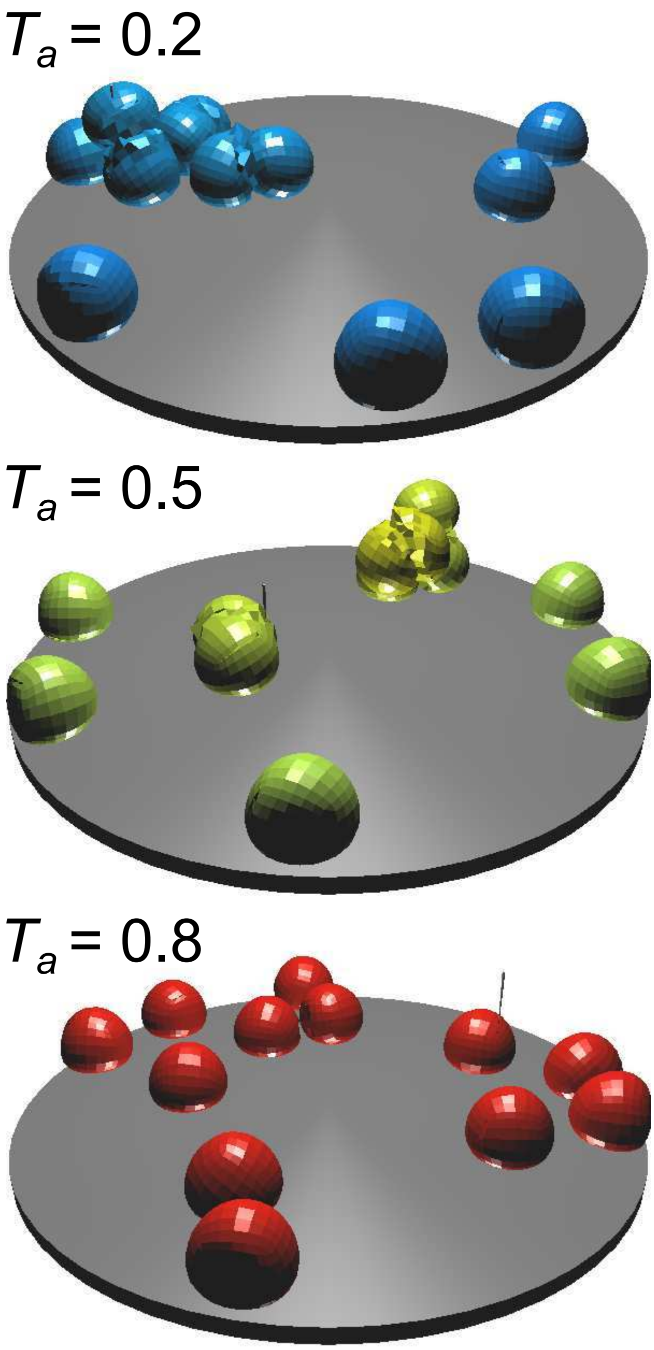

Fig. 1. Typical aggregation patterns self-organised at three ambient temperatures. Pups, simulated as soft-deformable bodies, huddle together in large stable groups in cold environments $T_a = 0.2$ (a stable cluster of 7 pups in the top left corner was maintained in this simulation), cycle between smaller subgroups at $T_a = 0.5$ (transient clusters of size 5 and 2 are visible), and disperse at higher temperatures $T_a = 0.8$. The body temperature of each pup T_b is indicated by the colour. Note that the preferred ambient temperature is $T_p = 0.6$.

$$\frac{dT_b}{dt} = G - k_1 A(T_b - T_a) - k_2(1 - A)\left(T_b - \sum T_c\right),$$

where the exposed surface area A is the proportion of points that are not in contact with another pup, $k_1 = 0.9$ and $k_2 = 1.0$ are thermal conductances and $G = 0.055$ is a constant rate of thermogenesis. The three terms on the right of this equation correspond to heat generation, heat loss, and heat exchange, respectively.

Homeothermotaxis, as described in the model of [6], involves moving continually forwards while turning in the direction that minimizes the discrepancy between a preferred temperature and the current body temperature. To define homeothermotaxis for the simulated pups in the present model we first define a reference vector in egocentric co-ordinates, as $\mathbf{v}_{\text{ref}} = [x_{\text{ref}}, y_{\text{ref}}, z_{\text{ref}}]$, which is of unit length and points from the center of gravity of all points $\mathbf{x}_{\text{cm}}$ in the direction of the (arbitrarily chosen) first point of the pup $\mathbf{p}_0$. A target direction vector $\mathbf{v}_{\text{target}} = [\cos\theta, \sin\theta, 0]$ is then computed in an allocentric reference frame, using the [6] model to determine the angle θ (in the plane parrallel to the arena floor) as follows. All points are rotated around an axis through $\mathbf{x}_{\text{cm}}$ that is aligned to the (allocentric) z–axis by angle $\arctan2(-y_{\text{ref}}, -x_{\text{ref}})$. Following this transformation, points lying in the positive x are defined as being on the 'right' of the body, and points lying in negative x are defined as being on the 'left' of the body. Note that performing this calculation before using the derived quantities to direct movements implicitly assumes that animals maintain an egocentric frame of reference, i.e., that they know which way is up.

The average value of T_c for afferents on the 'left' of the body is used to define the temperature on the left T_L, and likewise the average value of afferents on the 'right' is used to define T_R. According to [6], we define $S_L = (1+\exp(-\sigma T_L(T_p - T_b)))^{-1}$ and $S_R = (1 + \exp(-\sigma T_R(T_p - T_b)))^{-1}$, and

$$\Delta\theta = \arctan\left(v\frac{S_L - S_R}{S_L + S_R}\right),$$

where v sets the speed of rotation of θ.

Homeothermotaxis is then implemented by setting the components of the external force vector that is applied to the point cloud to be the components of $\mathbf{v}_{\text{target}}$, i.e., $\mathbf{f}_{\text{ext}} = \mathbf{f}_{\text{ext}} + [\cos\theta, \sin\theta, 0]$. The pup is essentially 'blown' in the direction of contacts that will bring its body temperature closer to the preferred temperature. Note that the only information exchange between pups occurs when they are in contact, and that homeothermotaxis involves no distal sensing.

Results

The model was implemented in c++ using standard libraries. OpenGL was used for visualisation. The armadillo linear algebra library was used, mainly for calculation of the (pseudo-) matrix inverse operations required for computing $\mathbf{R}$

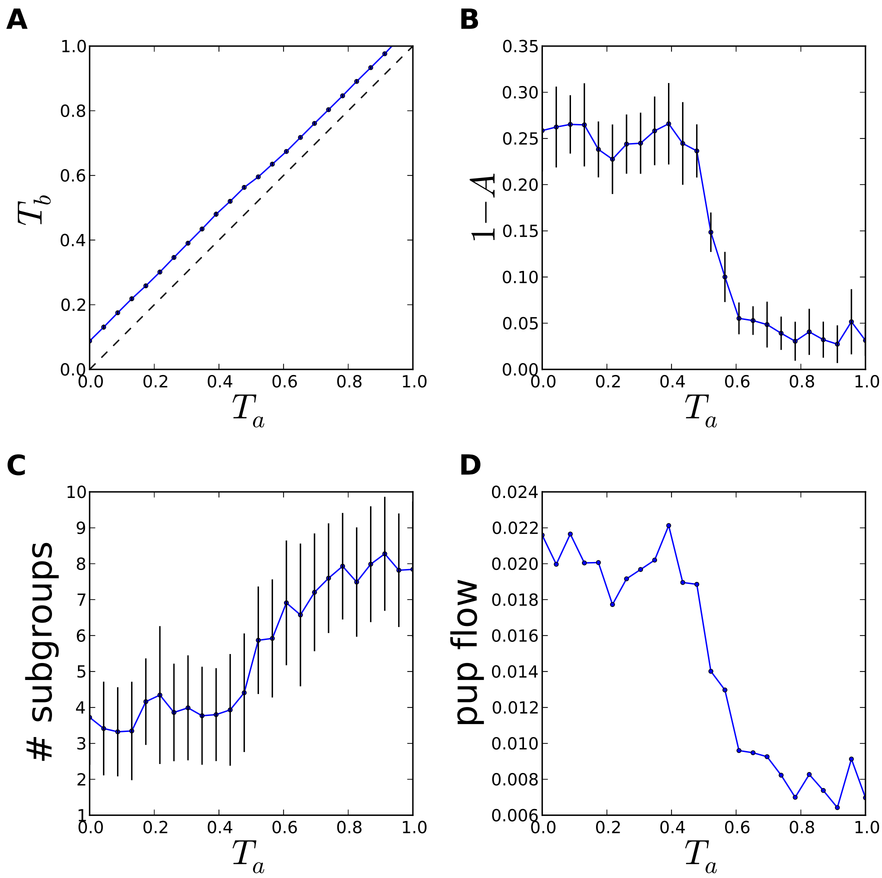

Fig. 2. Metrics of self-organising huddling. **A**. The average body temperature T_b is maintained above the ambient temperature T_a, when the ambient temperature is low. **B**. The average exposed surface area A gives a metric of huddling $1 - A$, which reveals a phase transition from huddling to non-huddling as the ambient temperature is raised. **C**. The average number of independent groups of clustered individuals increases as the ambient temperature is raised, showing that individuals group together in the cold and separate when it is warm. **D**. A metric of pup-flow, defined in terms of the variability in the exposed surface area, reveals a peak at $T_a \approx 0.4$, as predicted by earlier models.

in the shape-matching algorithm (arma.sourceforge.net). Python was used for analysis. The code is available by request.

Each simulation consisted of iterating the dynamics of the model through 1500 timesteps, and the first 500 timesteps (as pups fell into an initial pile) were discarded from analysis. At a given ambient temperature, ten simulations were run, each with the pups initialised at different random initial locations and different random initial orientations, and means and standard deviations were computed for each metric of huddling. Simulations were conducted at each of twenty four ambient temperatures $T_a \in \{0, 1\}$, corresponding to a range of approximately $0°$C to $50°$C. Figure 1 shows typical aggregation patterns formed at three ambient temperatures.

Metrics of huddling were i) the average body temperature T_b maintained by the group, ii) one minus the proportion of the exposed surface area (note that using $1 - A$ means that larger values indicate increased aggregation levels, i.e., stronger huddling), iii) the number of different subgroups, where a subgroup comprises all individuals that are connected either directly or via intermediaries, and iv) 'pup flow', computed as the absolute value of the derivative of the exposed body surface (see [16, 10]).

Figure 2 reveals a phase transition in the self-organisation of huddling behaviours in the group. This is revealed as raised body temperatures and low exposed surface areas at cool ambient temperatures, and a transition to the opposite profile as the temperature is increased. A central prediction of the thermodynamic description of huddling in related models is that at the critical temperature of the phase transition there should be a peak in the pup flow metric [16]. This prediction dervies from an analogy between huddling (measured as $1 - A$) as the energy of the system and pup flow as the heat capacity of the system, as these terms are defined in statistical physics [10]. The predicted peak in pup flow at the critical temperature of the phase transition is apparent in Figure 2 at an ambient temperature of $T_a \approx 0.4$.

Discussion

A self-organising model of thermoregulatory huddling behaviours, in which rodent pups were modelled as soft-deformable bodies, was shown here to recreate a phase transition in the degree of aggregation as the environment temperature was varied. Simply put, the model confirms that when it is cold a huddle will form and when it is warm the pups will disperse; at the critical temperature between huddling and dispersion, pup flow peaks, as predicted by earlier related models. This result confirms the behaviour of the earlier models [6, 10], which simulate the pups as two-dimensional rigid bodies, and suggests that a temperature-mediated phase transition is a robust feature of the self-organising interactions assumed by these more abstract descriptions of huddling.

The present result adds to a program of work in which thermoregulatory huddling has provided a lens on a range of questions about self-organisation. In what might be thought of as a *zero*-dimensional model, the litter were described using a single equation, allowing the effects of huddling on the evolution of a population of litters to be investigated in simulation [18]. In what might be thought of as a *one*-dimensional model, the litter were described as a system of magnetic spins fixed in position on a lattice, allowing the thermodynamics of huddling interactions to be understood with reference to the theory of Ising spin-glass models and statistical physics [10]. In what might be thought of as a *two*-dimensional model, the litter were described as a Vicseck system [19], as particles moving around in a 2D arena, and this model provides an important existence-proof that realistic aggregation patterns can emerge under basic assumptions about the physical interactions between animals [6]. The present model can be thought of as a further extension to *three*-dimensions, which may be used to explore how morphological factors constrain self-organisation in real systems of interacting animals.

The patterns of movement generated by animals during early postnatal development constrain the nature of the sensory signals that drive brain development, in particular in highly plastic structures such as the neocortex. For rats and mice, thermoregulatory huddling behaviours dominate the behavioural repertoire during the first three postnatal weeks, when the thermal physiology is maturing and the neocortex is most plastic. Movement of the animal introduces correlations between sensory receptors *within* a sensory modality, e.g., whisker deflection patterns are correlated by the movement of the face relative to tactile stimuli. Self-organising map models, based on local competitive interactions between neurons and Hebbian learning, explain how such correlations shape cortical circuitry, e.g., explaining somatotopic alignment between representations of whisker movement direction in the developing primary somatosensory (barrel) cortex [14]. As well as constraining the statistical structure within a modality, huddling also introduces patterns of correlation *between* modalities that might be captured by the same mechanisms of cortical map self-organisation in multimodal areas. For example, an orienting movement that allows a cold animal to contact a warm littermate on its left introduces correlations between touch (i.e., subsequent contacts made on the left side of the body), vision (i.e., a left-to-right optic flow pattern), audition (i.e., the sound of a contact, or the subsequent vocalisation of the littermate on the left), and correspondingly distinct vestibular and olfactory patterns. Importantly, during huddling these multimodal correlations are experienced in the context of thermo-tactile reward, hence via huddling cortical map self-organisation may be interrogated in a situation where the *function* of the maps may be clearly defined.

The rodent huddle has been suggested to be an ideal 'biohybrid system', in which synthetic littermates might interact with real animals in order to collectively thermoregulate [20]. To this end, ongoing work with the three-dimensional huddling model is investigating the relative contribution and interplay between a number of factors thought to influence the emergence of the huddle, including differences in body shape, relative body mass, and differences in the rates of thermogenesis, e.g., between males and females. Systemmatic manipulation of these factors in controlled simulations may reveal how the patterns of sensory and motor experience in the huddle constrain the inputs to the developing rodent brain. Reproducing similar mechanisms of brain development in the articifical neural networks of a synthetic littermate might enable it to learn to control and manipulate the self-organisation of a biohybrid huddle.

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