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This submission has been motivated by an invitation for the special issue: Rethinking cognition.

Highlights

- Movements can fundamentally transform the task for the brain.
- A same brain in different bodies or situations produces different behaviors.
- Clear-cut apparent decisions can arise without top-down control.
- A cognitive being may result from synchronization of distributed processes

Title: Embodiment, movements and the emergence of decisions. Insights from insect navigation.

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Abstract

We readily infer that animals make decisions, but what this implies is usually not clearly defined. The notion of decision making ultimately stems from human introspection, and is thus loaded with anthropomorphic assumptions. Notably, the decision is made internally, is based on information, and precedes the goal directed behaviour. Also, making a decision implies that ‘something’ did it, thus hints at the presence of a cognitive mind, whose existence is independent of the decision itself. This view may convey some truth, but here I take the opposite stance. Using examples from research in insect navigation, this essay highlights how apparent decisions can emerge without a brain, how actions can precede information or how novel goal directed behaviours can be implemented without neural decisions. This perspective requires us to shake off the idea that behaviour is a consequence of the brain; and embrace the concept that movements arise from – as much as participate in – distributed interactions between various computational centres – including the body – that reverberate in closed-loops with their environments. From this perspective we may start to picture how a cognitive mind can be the consequence, rather than the cause, of such neural and body movements.

Embodiment in ants

A first approach to highlighting the interplay between brain and body is to consider examples of embodiment, where cognitive problems are outsourced to body structures and movements.

Among classic examples of embodiments is our tendency to display hand gestures when solving a spatial reasoning problem, or to mimic facial movements when judging the emotion of others. Performing such gestures does improve performance, and, in contrast, preventing them or displaying other gestures non-related to the task decreases the cognitive performance [1–3]. If someone asks you the way to the train station, stand up and free your hands before answering, your choice of words will likely be better. However, these examples illustrate merely a facilitating role to the body. Body movements can be viewed as helpful but non-essential, and may not fundamentally modify the type of cognitive process involved to solve the task. Research in ant navigation offers starker examples of embodiment, where movements transform the cognitive problem and enable novel solutions to emerge. For instance, when a foraging ant is recapitulating a well-known route using learnt visual cues [4–6], she needs first to compare the currently perceived visual scene to its memory in order to recognise whether the location is familiar. If that so, the ant must then derive information about which is the correct direction to go. A priori, this task requires complex visuo-spatial representations

and abilities such as mental rotations or allocentric spatial reconstruction. Indeed, when engineers design robot that must follow a route, such as during the DARPA Grand Challenge race for autonomous cars [7], they resort to high accuracy sensors and impressively heavy computing power. Ants, in contrast, not only solve the same problem more robustly – they do not get lost – but do so in an apparently simpler way. Ants have low-resolution vision [8–10], their eyes are rigid and immobile, and they walk mostly forward, very rarely sideways. At first, such a reduction of sensory information and degree of freedom seem like a serious handicap. In fact, these bodily constraints are a key part of the solution. Low resolution can greatly facilitates the recognition of natural scenes – in addition to reducing memory load [11,12]. Second, the fact that their gaze cannot depart much from their walking direction ensure that visual input and direction of movement are profoundly linked. As a consequence, the recognition of a scene as projected on the insect eyes – that is, without the need for any cognitive spatial reconstruction – directly indicates that the body is roughly aligned in the same orientation as when the scene had been memorised in the first place [13]. In theory, all the ant needs to do is : first, memorise views while facing the route direction and second, when comes the time to retrieve the correct route direction, rotate on the spot and move forward as soon as the current view appears familiar [14,15]. This minimal model is supported by the fact that ants typically show such rotational scanning movements when trying to recover their route direction [16]. The trick is particularly obvious when these insects are dragging heavy items backwards: they regularly have to drop their precious load and scan around to retrieve the route direction [17,18]. To put it simply: physical rotations bypasses the need for mental rotations. With this embodied strategy, all that is left for the brain to do is to store and compare low resolution visual inputs encountered along the route. This simplified neural task can be readily achieved by brain neuropils called the mushroom bodies [19,20], a structure that is indeed necessary for learnt visual navigation in ants [21,22]. Overall, given these bodies and movements, a few thousand neurons is all it takes to recapitulate remarkably long routes through complex environments [14,19].

Evidently, the existence of these movements do not imply that the insect lack additional, more sophisticated neural abilities [15,23–25], which could be necessary for tasks requiring simulations beyond what physical movements can provide, or simply useful when producing such movements is too costly. However, through this example, one can envision how movements and body structures profoundly change the means to solve a problem. The neural circuit needed to store and compare egocentric low resolution views can be quite different –and arguably much simpler– from the one required for mental rotation or allocentric spatial reconstruction. Motor movements literally transform the information provided to the brain through sensors. After all, movements evolved before brains, and the first neurons to appear were used to coordinate muscles. This is the ground on which higher cognition is built. Scanning in ants, like human gestures when solving spatial tasks, are not just helpful tricks. They disclose a deeper, more fundamental way of functioning.

Same neural mechanism, different behaviours.

We have seen how body senses and movements can contribute to a successful behaviour, but what about a *change of behaviour*? Suitable changes of behaviours are typically thought to be the consequence of so-called ‘decisions’; but does this necessarily implies a dedicated mental process?

When recapitulating a route home, desert ants run remarkably fast and straight [4,5,26], but having arrived within close proximity of the nest, their behaviour changes drastically: they slow down and engage in convoluted searches for the nest entrance, similarly to what they do when in totally unfamiliar terrain [27–32]. ‘Route following’ and ‘goal pinpointing’ (also called ‘homing’) are two

different navigational tasks. While the first demands the ability to maintain a correct direction of travel, the latter requires one to pinpoint a very specific location, often by turning around. Therefore, it initially feels intuitive that two different mechanisms are at play, and this is probably why these tasks have been typically investigated separately ('nest pinpointing': [33,34,27,35,36,28,37,38]; 'route following': [4–6,37–40] and called for different types of models [6,15,33–35,41,42]. In fact, both behaviours may well emerge from the same mechanism. The trick, revealed by behavioural observations of ants, is again about movements rather than brains. Upon leaving their nest, ants (similarly to bees and wasps [43–47]) display well-choreographed dances around the nest where they regularly turn around to pause while fixating their gaze in a specific direction, such as the nest direction [48–51]. The same happens when the insect is departing from a food source; it turns around multiple times to fixate the newly discovered goal [52–54]. Assuming that ants memorise the egocentric scene perceived during these specific goal-oriented moments is enough for a goal pinpointing behaviour to emerge from the exact same minimal 'route-following mechanism' described above [14,55,56]. In other words, all around the nest, the 'remembered route direction' is a constellation of memories pointing towards the nest; so that a goal-centred search emerges naturally once the end of the route is reached. The rule is *always* to go straight when the view is familiar, without any need for additional mechanisms, but an apparent decision to start searching emerge.

Understanding this embodied way of functioning as proved remarkably powerful in insect navigation research. Based on novel experimental and neurobiological insights, this model has been developed further to capture a wider diversity of behaviours. Notably, assuming that ants also memorise aversive views pointing away from the nest [49,57], or categorise views as being to the left or right of the goal [58,59] can explain why ants behave similarly close to the nest and those on unfamiliar terrain [24], how ants could home equally successfully while walking backwards [60], or how landmark information could be readily combined with other heading information in the brain [59]. Even though these revised models explain a large number of observed behaviours and are more faithful to the insects' neural circuits, the mechanism remains in essence the same. The agent does not need to decide or even '*know*' whether it is close or far from its goal, yet its behaviour will still change appropriately.

The lesson from this body of work is that a suitable transition between different-looking behaviours may not necessarily result from neural top-down decisions, but can simply rely on the way the animal's body is –or has been– exposed to the environment. The learning walks displayed by naïve individuals illustrate well how this bodily factor participate to ontogeny and produce, *in fine*, behavioural diversity without the need to revise brain circuits.

The oscillating animal

If embodiment and environmental exposure – so-called situatedness [61]– favour the emergence of behavioural transitions within an individual, what about the more drastic differences observed across species?

Flying wasps [58] or moths [62,63], walking ants [24,64,65] or beetles [66], crawling larvae [67] or nematodes [68,69], swimming vertebrates [70,71] as well as moving cells [72], share a strange habit: they display regular lateral oscillations along their paths, slowly alternating between left and right turns and producing a zigzag trajectory. In insects, these oscillations are rather slow, with one cycle every five seconds or so and appear to result from neural reciprocal inhibition between left and right hemisphere's pre-motor conserved brain areas [62,73]. The ancestral and universal nature of lateral

oscillations suggests that they are fundamentally important across a wide range of insects with different lifestyles and body morphologies. But why?

Interestingly, when applied to ant visual navigation models, assuming that the body spontaneously generates oscillations drastically improves the efficiency of both route following [74] and homing [57]. In fact, all the agent needs to do is to modulate the amplitude of its oscillations based on the familiarity of the scene currently perceived... and it will safely go along its route and pinpoint home [57,74] (figure 1A). While unfamiliar views stimulate stronger lateral oscillations, and hence changes of directions, familiar scene inhibit them and thus favour movement in the currently facing direction. The mechanism is rather trivial, but the robustness of the emerging phenomena, whether for route following and nest pinpointing, is baffling. This model, in addition to being parsimonious, gain credence as it explains how aversive and appetitive visual memories are combined and captures particular movement signatures observed in ants [24].

Remarkably, keeping the same oscillatory model but swapping the eyes for olfactory organs, and providing a gradient of odour concentration instead of a visual world, leads to a very different but well-known behaviour: chemotaxis, that is, the ability to climb up odour gradients towards the odorous food source as observed in crawling maggots [67] (figure 1). Here as well, the model – now a model for chemotaxis – can readily explain how aversive and appetitive odour memories combine, and capture particular signatures observed in maggots. Notably, the agent, just like real larvae, may switch between two apparently different strategies, one where it approaches and circles around the source as if ‘orbiting’, and one where it displays a dense search by triggering strong turns and repeatedly crosses over the source [67,75] (figure 1B). As with the ant model, this behavioural switch does not result from a top-down neural decision, but arise from a spontaneous change in the ‘body movements-environment’ contingency: when orbiting around the source, the larva agent experiences little changes of odour concentration, which trigger only small turns biased towards the odour side and thus sustains the orbiting activity; however when close to the odour source, the gradient tends to be sharper, increasing the probability that the agent displays sharper turns that break the orbiting trajectory. Crossing over the odour source (rather than circling around it) leads the larva to experience stronger upward and then downward changes of concentration, and thus increases the likelihood of going straight and then displaying a sharp turn after passing the odour source (figure 1B). The novel behavioural regime is thus self-sustained in a sort of positive feedback (i.e., crossing over exposes the agent to situation that favour crossing over behaviours), but given some noise, the agent may still switch back and forth between both regimes [67].

Traditionally, chemotaxis and route following are considered fundamentally different behaviours, with the former regarded as simple and primitive, while the latter viewed as more complex [76]. It is true that both behaviours look different, happen at different spatial scales, concern different sensory modalities and species, and involved different cognitive demand: learning and comparing visual scenes appears wholly more complex than following your nose. However, these apparent differences in behaviour conceal the remarkable similarity in the mechanism that produce them: the modulation of a lateral intrinsic oscillator [20] (figure 1). Turns out, the similarity goes further. Ants and maggots do recruit homologous neural circuit to achieve these different looking behaviours. In theory, a larvae does not need the mushroom bodies to display chemotaxis, but in reality, they exploit the circuitry of this neuropil to learn which odour is worth following or not [77,78]. It seems that larva’s mushroom bodies continuously compares the currently perceived odour with previously learnt odours in a remarkably similar fashion than ants with visual scenes [20]. The strong behavioural difference emerge not so much from difference in neural circuitry, but from the difference in the movement-to-sensory relationships of vision and olfaction: oscillating paths allow for simultaneous

change in rotation and position, but while the perception of odour concentration is sensitive to change in position rather than rotation, it is the other way around for visual input [35].

It is astonishing that meaningful but different behaviours can emerge from a same neural machinery, embodied in different sensory environments (figure 1). Over large evolutionary time scales, designs that are easily malleable may be favoured. Distributed embodied systems, when based on oscillatory movements, offer such malleability and appear to have provided a fertile ground for the evolution of novel behaviours.

Do discrete behaviours mean decisions?

When we design toy robots or video games, each specific action is typically triggered by one specific command such as 'jump', 'crouch' or 'run'; and it may feel intuitive that it should be so for animals too. One example of such discrete behaviour is the ants' actual scanning behaviour discussed earlier, where the insects suddenly stop to rotate on the spot [16]. But could such clear-cut actions arise without clear-cut decisions?

By implementing the previously mentioned oscillation models on a robot ant (i.e., a smartphone with wheels and a panoramic camera), and realising it within a natural landscape to see whether it could recapitulate a learnt route, Kodjabachev and Mangan were surprised to see their robot occasionally displaying scanning behaviours even though there was no such command in the program [74]. The explanation is rather straightforward: in cluttered natural environments, the visual scene as perceived from the floor (at an ant's height) may become highly unfamiliar even after quite small displacements [79], and in Kodjabachev and Mangan's model, the more unfamiliar the scene, the more the robot's intrinsic oscillator is activated. Sudden perception of highly unfamiliar scenes strongly activates the oscillator and thus induce left and right turns that are so sharp that they physically override forward movement as the robot, like ants, will not drift sideways. That is, a scanning behaviour emerge. The apparent discreteness of the behaviour here does not result from a dedicated command, but from a non-linearity in the interaction between the robot and its sensory environment.

In *Drosophila* larvae, distributed bodily interactions suffice to explain the emergence as well as the transitions between a large panel of stereotypical actions, such as forward and backward crawling motions, stops or 'head sweep' behaviours – a larva equivalent of scanning behaviours. These actions are mostly derived from the body structure itself, aided by local neural loops that trigger muscle contractions to supplement the movement [80–82]. The body dynamics at play are not at a stable equilibrium, and transition between actions result from unpredictable, chaotic dynamics in the system. As the result, the model larvae explore its environment through a diversity of behaviour and apparent decisions that matches the one observed in real larvae, despite the absence of any neural mechanisms for gathering sensory information or triggering actions [81,82]. Remarkably, real larvae with genetically silenced brain activity equally display their usual panel of behaviours in a manner and frequency that seems indistinguishable from intact larvae [83], proving that the natural transitions between discrete actions do not require brain decisions.

Obviously, signals from the brain do influence behaviour, for instance, by modulating the forward speed or the oscillations' amplitude as in the route following or chemotaxis models mentioned above. Discrete actions such as head-sweeps (or scans), stopping, or resuming forward motion after a pause can be strongly favoured by a strong or a weak signal [84], but such signals should not be seen as discrete commands because 1- they are non-essentials for the action to emerge, 2-their

consequence remain probabilistic and 3-they operate equally at lower range in a graded manner, [85,86], reflecting the continuous nature of the sensory environment. In other words, apparently clear cut behaviours do emerge without clear cut decisions.

'I know therefore I do' and 'I do therefore I know'

We have showcased how a navigating ant does not need to know whether or not it is close to its goal to engage in the correct behaviour; similarly, a larva does not even need a brain to execute a whole panel of actions. However, '*Does not need to know*' does not imply '*Cannot know*'. Quite the contrary, the fact that a relevant behaviour can emerge – without prior awareness – provides an additional opportunity for the system to gather knowledge from the situation, by monitoring not only the environment, but its own behavioural state.

Evidence shows that insects do monitor their own behavioural state – whether through proprioception or efference copy – to modulate various regions of their brain. For instance, whether a fly is resting still, walking or flying, will differentially activate neurons in multiple brain areas, such as motion vision neurons in the optic lobes [87,88], direction sensitive neurons in the fan-shaped body of the central complex [89], or perhaps more intriguingly, dopaminergic neurons conveying positive or negative reinforcement in the mushroom bodies [90]. Not only: “I see danger therefore I’m flying away”, but also: “I’m flying away therefore there might be danger”. Both are probably true, and the system is surely most effective if cause and consequence are reverberating in a closed-loop (figure 2B).

In this way, movements during sequential inspections of visual patterns can provide a simple solution for bees to solve discrimination tasks or complex concept learning paradigms, eschewing the need to extract the shape or concept per se [91–93]. Similarly, human patients with visual agnosia may not recognise objects but can still perfectly adjust their grasping movements to seize them, as the action involves a different neural pathway [94]. We can see how monitoring their own movements could provide information about the size or orientation of the object, and thus transcend what is available to them through direct perception of the external world.

Perhaps a most demonstrative example of the transcendental propriety of self-monitoring is path integration. During navigation, the ability for path integration is nothing else than monitoring one’s own movements to estimate its position relative to a starting position. This internal estimation, in addition to enable returning home and displaying shortcuts, can serve as a scaffold for the establishment optimal routes passing through multiple goals, a behaviour that is usually assumed to involved a mental map or knowledge about the relative position between the goal themselves [95,96]. Whether insects do or do not possess this knowledge is another debate [97,98], but what is certain, self-monitoring can bypass the need for complex reconstruction of the world.

What difference does it make to the system whether the informative signal comes from the environment via an external sense, or from the body via an internal sense or motor copy (figure 2B)? After all, the body can be viewed as a perceptual environment, one that can be particularly well controlled.

Is there a ghost in the machine?

The works presented here point at a distributed and dynamic nature of behavioural control (figure 2B), which contrast strongly with our intuitive sense of a cognitive being, in the sense of a higher awareness – or ghost in the machine – resulting from a global integration of information and producing top-down decision (figure 2A). However, both views are not necessarily mutually exclusive.

Perhaps a promising research for tackling the existence of such top-down decision is the study of attention-like processes, for which a ‘selection’ in the brain must precedes behavioural choices. There is strong evidence for such processes in insects [99,100]. Insects can ‘focus’ on specific cues and ‘disregard’ others not only based on the current sensory cues themselves (which can be achieved through neural filtering and winner-takes-all competition, forming a so-called bottom-up control of attention) or their own behavioural state (previous paragraph), but also based on their past experiences and current internal state. For instance, a fly will recall olfactory memories and track an odour previously associated with food only if it is hungry [101]. Similarly, a larva will not bother recalling olfactory memories associated with sugar, if sugar is already present in the environment [102]. Likewise, depending on its motivational state, an ant will recall either food-ward or homeward visual memories and disregard the other [103,104].

One key question is whether such ‘internal’ decisions result from local and specific gating mechanisms or from a global information integration. The latter could be implemented in brain-wide networks of highly connected neurons such as the so-called ‘rich club’, which we observe in human [105] but also animals including insects or nematodes’ connectome [106–108]. However, evidence in insects rather support the former. For instance, neurons releasing the neuropeptide F, which convey specific homeostatic information such as lack of a given nutrient, modulate equally nutrient-specific dopaminergic neurons, thereby *directly* gating the learning and/or expression of the memories associated with this specific nutrient need [101,109]. Some internal modulations have less specific targets: hormones and giant neurons innervating multiple regions can diffuse information throughout the brain to modulate behaviour [110–113]. But here also the information transmitted is more direct and situation specific than the product of a brain-wide like integration process; and the consequence on behaviour is more probabilistic than the result of a clear cut decision.

But then, what would the role of ‘rich club’ like brain-wide networks be? Instead of – or in addition to – ‘integration’, these networks may be key for ‘synchronisation’ of neural activity across far-flung regions [105,107,108], thereby imposing the coherence underlying attention [114] at a larger scale. Rather than decision centres, perhaps such networks can be viewed as blind orchestrators, crystallising the many local and specific ‘decisions’ achieved in different parts of the brain-body-environment system into a globally co-ordinated, and thus meaningful, activity (figure 2B). This neural resonance may well support a rich subjective experience, and hence, a cognitive being. If that is the case, the cognitive being would be more the consequence of a democratic poll than a monarch imposing decisions.

Conclusion

The minimal models of insect navigation presented here illustrate the power of dynamic and closed-loop processes, where behaviours arise from distributed interactions between brain, body, movements and environment, where the distinctions between internal or external source of information is blurred, and the notions of cause and consequence are supplanted by the one of emergence. These processes enable clear-cut actions and appropriate shift in behaviours to happen despite worryingly simple neural mechanisms, far removed from what we could call decisions. As a

corollary, they provide insight into how novel behaviours can arise along ontogeny and evolution without much change in the underlying mechanisms.

The motivation behind this approach is not to assume that insects are non-cognitive beings, but to seek the most parsimonious explanation behind these apparently complex phenomena, while departing as much as possible from our anthropomorphic intuitions [115]. However, one should keep in mind that it is our models that have simple brains, not the insects; and this approach is not mutually exclusive to a more cognitive view. On the contrary, the distributed mechanisms presented here form a formidable basis on which higher level decision-making could operate, as they produce meaningful behaviour that can be readily modulated given minimal variation in neural activity. Also, such distributed systems might need to be globally synchronised to be operational on a given task. Rather than a ghost in the machine taking decisions, perhaps it is the need for such a synchronisation, implemented through richly connected neural networks imposing a system-wide resonance, that may provoke what we could call a cognitive being.

Figure legends

Figure 1. One neural mechanism, multiple behaviours. A variety of functionally relevant behaviours can arise from a same algorithm based on an intrinsic oscillator embodied in different sensory-movement contingency. A) Given panoramic visual scene as input, the algorithm (left) will result in route following or nest pinpointing behaviours depending on the movements that were achieved during previous learning stage. (Red dots: overall path taken by the agent in a realistic reconstructed visual world [116], as modelled in [57]). B) Given olfactory receptors able to detect change in odour concentration, the same neural algorithm (left) can produce two different chemotaxis behavioural regimes that self-sustain purely because of body movements-environment contingency. (blue dot: odour source; blue lines: isoclines of odour concentration; dark dots: overall path taken by the agent, as modelled in [67]). A,B) Both models can involve the same circuitry based on the insect's mushroom body [20]. Changing the nature of the sensory input suffice to switch from visual navigation to chemotaxis behaviours.

Figure 2. Two non-mutually exclusive views of the flow of information underlying an organism's behaviour. A) The first scheme highlights integration of external world information and subsequent top-down decisions. 'Rich-club' brain-wide neural networks may achieve a global integration of information to support a cognitive being that actively produce decisions (green). B) The second scheme emphasizes parallel and reverberating closed-loop processes, body/environment interactions as well as the distributed and self-emerging nature of decisions. A cognitive being may arise from a need for overall coherence of the system through synchronisation (and hence selection) of process activity, which could be achieved by 'rich-club' brain wide networks (in green).

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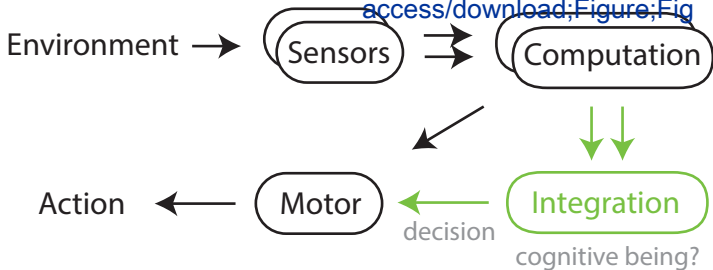
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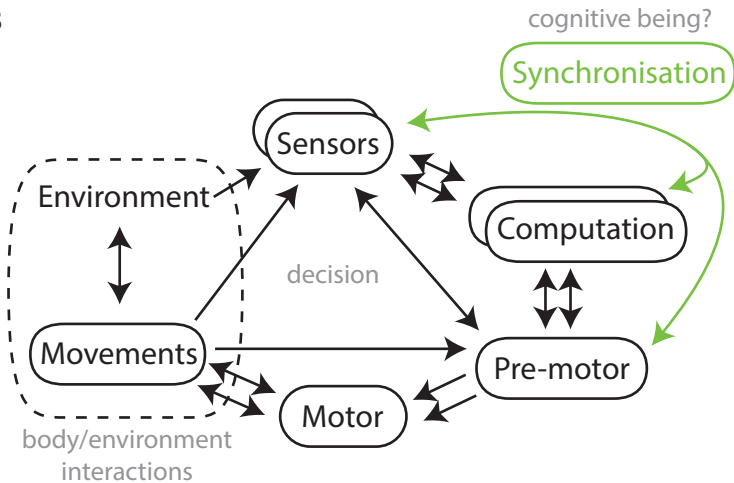
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Figure 2

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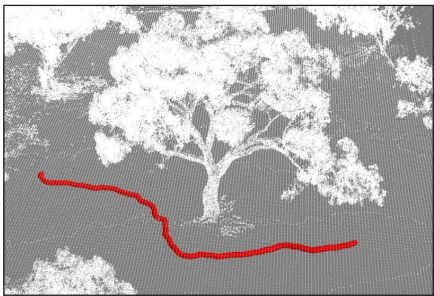
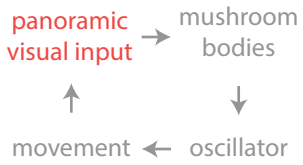
B



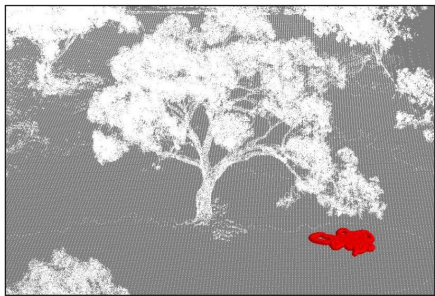
A Visual navigation

Route following behaviour

Goal pinpointing behaviour



different ontogeny
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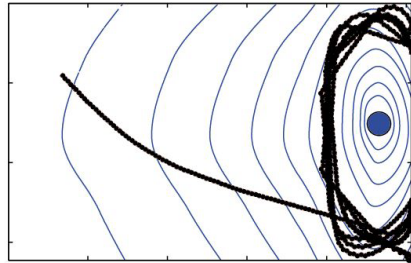
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different sensory world

↖ same ↗
algorithm ↘ ↙

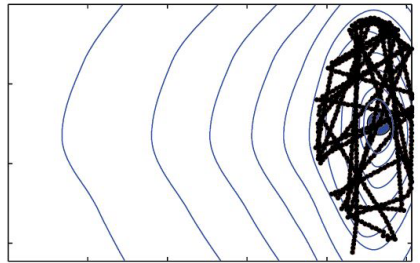
B Chemotaxis

Orbiting behaviour

Crossing-over behaviour



different body/environment contingency
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The author declares no conflict of interest