Chapter 6
Towards neural reusable neuro-inspired systems

Abstract This chapter presents an overview of some key aspects of the neuro-inspired modelling previously discussed, under the new perspective of the *neural reuse* theory. Here it is envisaged that the excellent capabilities shown by insects with their small neuron number and relatively low brain complexity, as compared to vertebrates, could be justified if some key neural structures are re-used for different behavioural needs. The chapter recalls some examples, found in the literature for addressing specific topics and reformulates them in relation to the neural reuse theory.

6.1 Introduction

In order to design and realise bio-inspired cognitive artefacts, a deep understanding of the mammalian brain would be necessary, which is still lacking. On the other hand, even the most sophisticated robot does not possess the ambulatory or cognitive capabilities of insects like ants, bees or flies. Already here an open question on the actual working of neurons and neuron assemblies arises: how can such tiny insect brains cope in such an efficient way with the high number of parallel exogenous and multimodal stimuli they are exposed to? A straightforward answer would be to try, exploiting results of focussed experiments, to build a block-size model made-up of interconnected sub-systems. Each block in this model would represent a specific part of the insect brain related to a specific behaviour and one would try to build a meaningful network of connections among them. The final figure that arises from this strategy is to build a cooperative-competitive dynamical system which would combine all the modelled behaviours, designed and implemented basically as a superposition of dissociable functional components. This is indeed what is already done in literature and the approach is powerful and valid for modelling most of the sensory-motor direct pathways and related processing. Some recent European projects were focussed toward building an insect brain computational model based on such type of approach [2]. But it is true that complex behaviours need a number of tasks to be

implemented concurrently, not in competition, but rather in cooperation. Moreover, studying in details the peculiarities of the neural structures in charge of eliciting particular behaviours, an idea was conceived that a block-size perspective in modelling the insect brain could be considered somewhat restrictive, since it potentially could not exploit the richness of dynamics generated in particular substructures of the brain. Particularly the dynamics of the MBs should be efficiently exploited in other parts of the brain to generate complex proto-cognitive behaviours. MBs, often homologized with the mammalian limbic system, where ancestral perception and emotions are forged, are the centre where learning mechanisms were first identified in the insect brain. There, memories are formed and used to build sensory-motor associations. From these facts the idea emerged to look at the insect brain from a holistic view. The complex dynamics present in some parts of the insect brain, like the MBs, could be seen as a place where complex spatio-temporal patterns of neural activity are formed, to be used concurrently for a number of different behavioural responses. This will happen presumably in cooperation with other parts of the brain which can exploit such dynamics and can, in principle, be much simpler than the MBs. This idea has a lot of features in common with the concept of *neural reuse*, recently introduced by Anderson [1]: central neural lattices could be massively reused for contributing to different behaviours, thanks to variable connections. This concept, drawn from a high level, psychological perspective, can be reflected into a low level view: the same neural structure can have different uses according to which part of its dynamics is exploited to match the outer-world needs. For instance, locomotion control in a legged robot is a particular case of ground manipulation and implies concurrent motion of different parts of the body. On the other side, perception-for-action implies an abstract manipulation of the surrounding environment to reach an ultimate goal. Examples of this concept can be found in the insect world: cockroaches can easily shift from basic hexapedal to a fast running bipedal locomotion, whereas dung beetles perform manipulation and transportation with front and mid legs while walking with the remaining two legs. To conceive new paradigms for the representation of these behaviours from a neural circuit viewpoint, we have to refer to known facts from the insect brain processing areas. Insect data are primarily available from physiology (including also microsurgery) and behaviour research in honeybees, grasshoppers and cockroaches. For *Drosophila* flies rich data based on various techniques like calcium imaging, neurogenetic manipulation, or biochemistry of plasticity (chapt. 1.3), are also available. MBs are the necessary centres for olfactory classical conditioning and are the site for keeping aversive and appetitive memories of odours on different time scales. They have later been implicated in other forms of learning (visual, motor, classical and operant conditioning) and classification tasks (visual foreground-background discrimination, disambiguation of contradictory visual cues), also in motivation control [14] and sleep regulation. Very recent methods in *Drosophila* neurogenetics [4] allow to genetically drive the activity, or silence the output, of single cell types for most, if not all of the MB neuron types individually.

Taking inspiration from *Drosophila melanogaster*, and from insects in general, their most important exteroceptive senses, used to acquire information from the en-

vironment, are olfactory and visual perception. Olfactory and also visual processing are two fundamental sensory modalities used by insects for food retrieval and predator escaping. The fruit fly detects food sources and identifies dangerous substances mainly through its olfactory system. The sensory information acquisition starts from the antenna where several chemical receptors are located. Subsequently through the antennal lobe the acquired signals are conveyed via the projection neurons to the mushroom bodies (MBs) where the mechanisms of learning and memory for odour classification and behaviour association have been identified.

Besides the peripheral processing centres for vision and olfaction, the MBs are the insect central brain structure with the best-described wiring and physiology; they are key structures for different forms of insect learning. Judged by the expression pattern of early neurodevelopmental genes, MBs are the insect orthologue of the human hippocampus (underlying declarative learning and spatial memory) and amygdala (underlying fear, emotions and the memory for hazards) [17].

The other sensory modality, massively used by the fruit fly to orient itself in the environment, is vision.

Visual stimuli are acquired by the compound eyes and, after processing by the optic lobes, they reach, via the optic tubercles, the central complex. Here particularly the protocerebral bridge, the fan-shaped body and the ellipsoid body are the substructures involved in visual orientation [18] and in visual learning mechanisms based on classical conditioning [12].

Notably MBs and CX are the most important and well-studied insect brain centres and only recently direct connections among them were identified (see chapter 1). Another important sensory modality less studied in *Drosophila* but deeply investigated in other insects like stick insect [6] and cockroach [19] is related to the tactile sense. Mechanosensors are distributed all over an insect's body and allow a direct interaction with the environment during walking and also during flying. Of particular importance are mechanosensors in the body appendages, foremost in the antennae. Due to the massive presence of mechanoreceptors, the processing of this information is performed in a decentralized way and to large parts in the thoracic ganglia (part of the central nervous system) to create local feedback for reflexes and other simple reactive strategies. Nevertheless as for the other sensory modalities, part of the acquired information is transferred to the central brain and very recently, experiments show that the CX is involved in handling this information. In particular the PB seems to be responsible for orientation strategies in presence of tactile stimuli. These information are the basic facts that show how different neural centres cooperate in performing different behavioural tasks controlling the same neural circuits. Cooperation and exploitation of multiple complex dynamics is then the common denominator of this new way of looking at the insect brain.
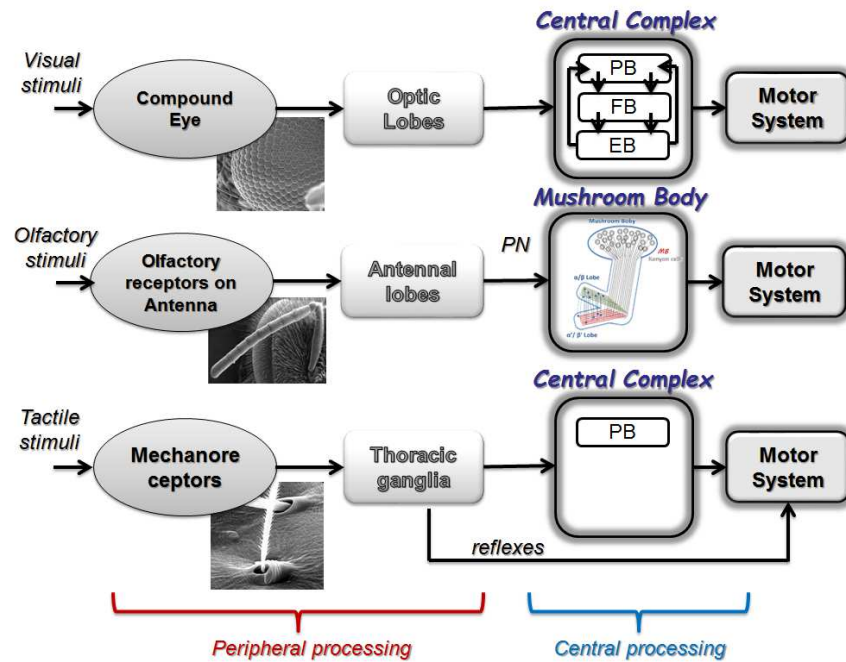
Fig. 6.1 Block scheme of the centres involved in the management of different sensory modalities: visual, olfactory and tactile. A central and a peripheral portion of processing is present in the identified sensory paths.

6.2 Multimodal sensory integration

The different sensory modalities present in insects are processed following distinct pathways from the periphery to the central brain even if some local shortcuts can be observed in the case of reflexes. The interaction among the modalities is needed to have the complete portrait used to perform behavioural choices.

A scheme of the most important processing stages for each sensory modality in *Drosophila* is shown in Fig. 6.1. The sensory-motor loop mainly involves the MBs for olfactory stimuli whereas the CX is strongly involved in the processing of visual and tactile stimuli. For all the reported paths a central and a peripheral processing phase can be distinguished.

A detailed scheme of the neural centres involved in the processing with particular attention on the different orientation behaviours triggered by the available sensory modalities or combinations thereof is depicted in Fig. 6.2. The different sensory receptors are distributed along the body and the information acquired is processed by several interconnected neural centres. Considering the compound eye, the photoreceptors acquire visual information that is transferred via the optic lobes to the CX that can trigger motor activities by sending commands to pre-motor areas. The an-
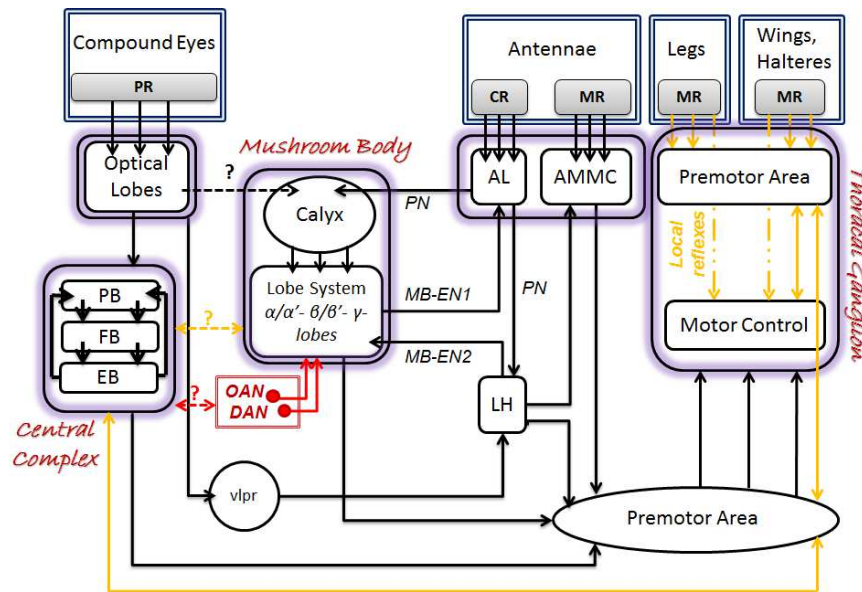
Fig. 6.2 Block-size model of the neural centres involved in orientation behaviour triggered by different sensory modalities: visual, olfactory and tactile. Visual stimuli are acquired by the compound eyes via photo-receptors (PR) and, after a pre-processing at the level of the optic lobes, are handled by the CX that decides the motor commands to allow a visual orientation behaviour. Olfactory stimuli are acquired by the antennae via chemical-receptors (CR) and through the antennal lobes (AL) and the projection neurons (PN) reach the MBs where mechanisms of learning and memory are performed through reinforcement learning signals via dopaminergic neurons (DAN) and indirectly via octopaminergic ones (OAN). Tactile stimuli are acquired by mechanoreceptors (MR) distributed along the whole body. High numbers are found in antennae, legs and the halters which are used for flight control. The information coming from sensors distributed on legs and on the main body, can be processed locally by the thoracic ganglia for the generation of local reflexes, however, an interaction with the CX is also envisaged and in particular the PB seems to be involved in orientation strategies based on mechano-sensory modality.

tennae include multiple receptors processed by distinct centres. Chemical receptors located in the antennae are connected to the antennal lobes that, via the projection neurons transfer the acquired signals to the lateral horns (LH) and to the MB calyces. The LH is directly connected to the pre-motor area for inborn responses to olfactory stimuli [15] and provides a delayed event-triggered resetting signal to the lobe system [13]. On the other hand the MB lobe system provides feedback to the AL to filter the input creating mechanisms like attention and expectation. Conditioned learning can be obtained both in MB and CX using unconditioned stimuli from octopaminergic and dopaminergic neurons. The antennae are also the place of mechanoreceptors as for instance the Johnston's organs (JO), the fly's antennal hearing apparatus, used for sound and wind detection. The neural centre involved in the processing is the antennal mechanosensory and motor centre (AMMC). The interaction between visual and olfactory-based orientation is obtained via the ventrolateral

protocerebrum (vlpr) that mediates the transfer of parts of the visual information to the LH. This multimodal sensory integration is confirmed also by experiments where, in absence of a well contrasted visual panorama, olfactory orientation is not obtained [9]. Finally, mechanoreceptors placed in the main body and on the legs are handled by the thoracic ganglia where local reflexes can be performed. Moreover, part of this information can be transferred to the CX and in particular the role of the protocerebral bridge seems to be fundamental for mechanosensory-based orientation.

Duistermars and Frye analyzed the interaction between wind-induced and odour-induced orientation [9]. The presence of wind passively rotates the aristae on the antennae, stimulating the JO neurons that, via the AMMC trigger an upwind orientation behaviour. In presence of an odour gradient, the olfactory receptor neurons on the antennae trigger an orientation response from the MB/AL system and the LH-AMMC connection allows the use of the same orientation mechanism know for wind-induced behaviour. In fact the AMMC, via the antennal motor neurons triggers the movement of the aristae that activates the previously introduced orientation mechanism. This example shows, how apparently different orientation strategies can use the same neural circuitries for the generation of the behavioural response.

The known information about the sensory processing phase in the fly will be discussed in the following with particular attention to mechano-sensors that will have a significant impact on the implementation of locomotion control systems.

6.3 Orientation: an example of neural reuse in the fly brain

Orientation is a fundamental requirement for insects that need to use sensory information to reach food sources or to avoid dangerous situations. Different sensory modalities can use the same pathways for eliciting motor actions, so as to avoid the duplication of neural mechanisms that can be easily shared. The main facts known from biology are reported below.

6.3.1 Role of CX in mechanosensory-mediated orientation

To understand the role of higher brain centres in handling mechanosensory information, different experimental campaigns were performed. The idea was to limit the variables responsible for the fly behaviour only to mechanosensory information. A scenario taken into consideration consists of a fly, forced to move in the forward direction when an air shot is used to stimulate the movement. The wild-type fly behaviour consists of a change of its direction of motion whereas mutant flies of the CX are less reactive to the shot and quite continuous in performing the on-going behaviour. Going deeper into details through the involvement of several mutant lines, the central role of the PB emerged. Experiments with PB mutant flies, show how an

even tiny defect in part of the PB drastically modifies the fly orientation behaviour in response to these tactile stimuli.

It is interesting to notice that the fly's CX is a well-known centre for orientation in insects, deeply studied with respect to the visual sensory modality. In practice, there is a topological neural mapping between the fly's visual field and the particular PB glomerular structure. On the other side, in new experiments an intact PB is needed to perform a suitable orientation behaviour in response to mechanical stimulation.

This fact is of fundamental importance in view of the concept of neural reuse: the PB participates sector-wise to visual orientation and, as a whole, to mechanosensory induced orientation. The PB is then involved concurrently (i.e. re-used) for different tasks.

Looking at other insect species, there are examples in literature where the role of the PB is not only limited to visual orientation with regard to landmarks and objects: locusts are an example where polarized-light based orientation needs an intact PB. Therefore the PB can be considered as a quite general centre involved in orientation behaviours where different sensory modalities can compete or co-operate with each other. Visual orientation requires a topographical map within the PB, whereas mechanosensory processing, in principle, does not. However, a touch of frontal body parts prompts the fly to escape backward, whereas a touch of rear body parts would trigger escape in the heading direction. Moreover, wind-sensing is direction-sensitive.

Whether or not mechanosensation makes use of a topographical representation in the PB, there is a possible need for integration with the visual sense within the PB glomeruli and mechanosensory orientation will need a complete PB structure, too. Admittedly, this issue requires further investigations through experiments. Another important aspect to be considered is related to the coordinate transformation between the map of mechanoreceptors on the body and the Cartesian direction in the world related to orientation and escape strategies.

After these considerations, experimental evidence in the fly suggests a possible involvement of the CX in a mechanosensory pre-processing focussed on orientation. In fact, whereas thoracic ganglia are responsible for eliciting a family of basic reflexes directly and locally to the leg system, on the other hand, signals, whose specific pathways are up to now unknown, reach the PB, which acts as a higher level orientation controller. This hypothesis is in line with the preliminary experiments presented, where flies show escape behaviours upon both touch and visual stimuli. The touch sensors in the leg can therefore elicit local stimuli in the thoracic ganglia (and so also in the leg-wing system), but also reach the PB in order to elicit orientation strategies normally used in visual orientation. This will become clearer after the following paragraph, which clarifies the role of mechanosensors in olfactory orientation.

These preliminary analysis can guide the formulation of a plausible model for a mechano-sensory orientation strategy.

6.3.2 Olfactory and mechanosensory-based orientation

Thanks to olfactory orientation endowment, the fruit fly is able to track odour plumes under difficult wind conditions as well as under time-varying visual conditions. At the same time odour recognition takes place through a series of processing stages.

Recent studies [7] demonstrate that following an odour plume is not a simple task; at the same time also mechanosensory and visual inputs are required during flight. In fact, it has been shown that if an insect flies within a uniform visual panorama where high-contrast visual stimuli are absent, it is no longer able to orient toward the odour plume.

Multisensory integration is therefore an important ingredient of the fly behaviour as also shown in the model proposed in [11].

During the processing of olfactory signals, the olfactory receptor neurons (ORNs) transfer the acquired information to specific glomeruli in the AL (see Fig. 6.2). Moreover, projection neurons (PNs) connect the AL to either the LH or the MB calices. The LH is believed to receive also visual information from the ventrolateral protocerebrum (vlpr in Fig. 6.2): both visual and olfactory signals are delivered to the antennal mechanosensory and motor centre (AMMC) [7]. Antennal motor neurons arising from the AMMC, are also assumed to innervate muscles actuating the antenna.

On the other side, the passive motion of the antennae induced by wind stimulates neurons controlled by Johnstonorgans (JO) situated in the area of the antenna cuticle which is deformed by air motion. This activates different areas of the AMMC. Interestingly, it is argued in [7] that the increased activation of the left (right) ORNs and PNs in response to an odour on the left (right) and via LH-AMMC neurons triggers an asymmetrical activation of the antennal motor neurons (AMNs) arising from the AMMC which, via antennal muscles actively rotate the antenna segments, mimicking a passive wind stimulus and using the same neural assemblies to trigger a leftward (rightward) AMMC mediated motion. This hypothesis, directly supported by experiments and by the neuroanatomical model of the olfactory orientation system, leads to include a direct interaction between mechanosensory-mediated orientation and the olfactory orientation. It is interesting to notice, how mechanosensors can trigger also orientation behaviours. On the basis of the models and experiments discussed, tactile information follows the same paths used by olfactory and visual stimuli to perform orientation strategies. The same neural structures are therefore shared and used for different behavioural tasks.

In this complex orientation task, also visual stimuli are required, as outlined above. As is well known, the higher processing of visual orientation is mainly handled by the CX that can guide the insect towards the most attractive object in the visual field. Flies are attracted by the nearest object located in the frontal part of the visual field, whereas an object seen on the periphery of the visual field ($[-140°, -170°][140°, 170°]$) triggers an escaping reaction. As already mentioned in the book, the fan-shaped body (FB) is the area where rewarding and/or punishing visual features are learned and memorized. The path followed during olfactory ori-

entation starts from the olfactory receptor neurons that project to the antennal lobes. The LHs are responsible for the inborn, mostly reflexive behaviours triggered by olfactory signals, whereas the MBs are the centre where olfactory associations are created through reward- and punishment-based learning.

Olfactory-gradient orientation, in particular for a flying insect, as recalled above, is not obtained in absence of visual stimuli (i.e. when an uniform visual panorama is present). The LHs are also generating event-driven inhibitory input for the MB through extrinsic neuron connections (MB-EN2). Functional feedback connections from MB lobes centrifugally out to the AL via extrinsic MB neurons (EN-MB1) are also part of the system: a gain increase in the AL caused by this modulatory influence is at the basis of the formation of expectations.

For olfactory and mechanical stimuli acquired from the antennae, also the neural paths used for visual-based and tactile-based orientation are shared.

Looking at the CX in detail, in Fig. 6.3 a block-size model of the integration between the visual system and the mechanosensory system is depicted. From behavioural experiments and neurobiological analyses [10, 18], some roles of each subunit of the CX for visual learning and orientation have been identified. The fly's visual field, in the azimuth range $[-170^o, 170^o]$, is acquired by the compound eyes and relevant information are transferred from the PB to the FB for the generation of control signals sent to the ventral lobe for solving visual orientation tasks. The EB holds a short-term spatial memory. When the chosen target is temporarily obscured in the field, the EB projects a ghost copy of the missing object to persist in the following action for a while until new reliable information can be acquired by the sensory system.

In relation to mechano-sensors located on the insect body and legs, we can distinguish two main paths: a local handling and a transfer to higher brain centres, where orientation behaviours are elicited. Mechano-sensors are fundamental for the acquisition of the information needed during locomotion to coordinate and stabilize the walking gaits [8, 5]. In the presence of a tactile stimulus (e.g. an air shot) on a leg, the fly, depending on the intensity of the stimulus, either shows a local reflex like cleaning behaviour performed on the stimulated leg by an adjacent one or performs a repulsive orientation behaviour trying to avoid the source of the undesired contact. The orientation behaviour is obtained by transferring the local tactile information to the brain. From neurogenetics experiments the role of the PB in this process has been identified and this verifies the hypothesis that already existing neural paths can be reused for different sensory modalities, also taking into account that multiple stimuli can be integrated to take a decision.

In conclusion, the distributed sensory system and the neural structure devoted to handle this multimodal input are at the basis of the behavioural response in insects as well as in other animals. Taking into account the currently available information on the neuronal structure of *Drosophila melanogaster*, a plausible model of the dynamics involved in sensory processing mechanisms has been designed and discussed. The sensory modalities taken into consideration are those ones largely used by insects to survive in unstructured environments: olfactory, visual and tactile. The processing stages identified in the proposed model underline the basic principle ac-
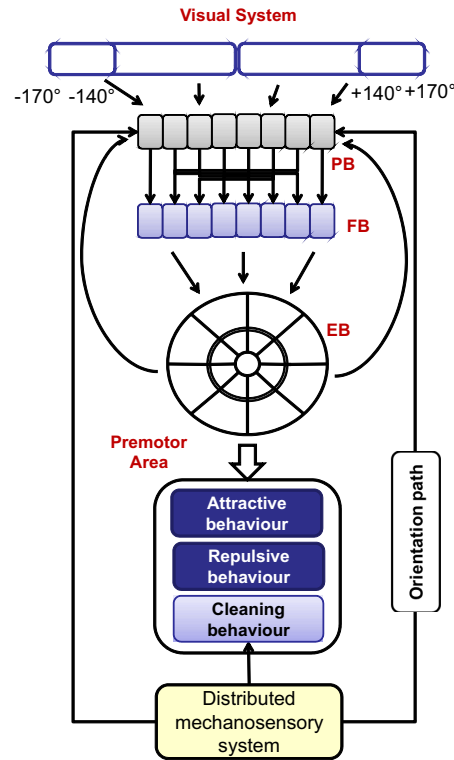
Fig. 6.3 Block scheme of the role of CX in visual and mechanosensory information processing. Visual information is handled by the protocerebral bridge (PB), the fan-shaped body (FB) and by the ellipsoid body (EB). The PB is mainly responsible for spatial identification of objects and targeting, in the FB the object features are stored and a meaning is associated to them using rewarding or punishing signals. The EB is responsible for spatial memory and in absence of fresh information, the object of interest can be tracked. The distributed tactile system can either locally trigger behavioural responses like cleaning behaviours or transfers the detected event characteristics to the PB, where orientation behaviours can be initiated as happens in presence of visual targets.

cording to which different sensory modalities are processed, at least in parts, within the same neural circuitries. In particular the orientation behaviours follow different neural paths: through the AMMC if the antennae are involved (e.g. olfactory and wind induced behaviour) and through the CX in presence of visual stimuli and tactile events detected on the insect legs.

6.4 Concluding remarks

The examples reported in the previous sections of this chapter clearly show that in *Drosophila*, neural circuits, established for one task, are re-used and exploited for

different tasks. In the animal kingdom, this transformation or adaptation, as Anderson introduced it, can be attained either during evolution, or during the development of the individual [1], without necessarily losing the original functionality of the neural circuits. This is exactly our case, where, not considering here which functional sensory-motor task has evolved before another during the early stage of the animal evolution or ontogeny, the different functions of the same neural structure are maintained to serve the specific behavioural needs. On the other side, it is well known in the mammalian brain that high-level cognitive functions require the cooperation and the concurrent activation of different areas of the brain typically devoted to other functions. This is of course a typical case for complex dynamical systems, where the single unit shows a non-linear dynamics which could be completely different from that one shown by the whole system. The massive re-deployment of neural structures is evident in higher brains, but it is difficult to be inspected in details. So, *Drosophila melanogaster* is an optimal candidate for this type of investigation, given its small brain and somewhat simple organization. But the smaller the brain, the larger is the need for reusing neural structures that are already working. Insect brains have a suitable size to investigate neural reuse in action. In the course of the chapters of our book first preliminary models for addressing spatial memory, motor learning and body size were introduced, followed by a model in chapter 5, that is able to cope with such tasks as motor learning, decision making, sequence and sub-sequence learning all-in-one. The common denominator in solving these diverse tasks is a unique core, a model of the structure and dynamics of the MBs, that has been considered as a specific multifunctional structure, that is at the basis of a number of different behavioural tasks that can be implemented concurrently. This is relevant, since MBs indeed are known to take a key role in many other functions than olfactory learning and memory (as seen in chapter 1). The computational model presented in chapter 5 was conceived to emphasize the role of MBs as the specific place where multi-modal associations are formed. The rich, spatio-temporal dynamics formed therein, potentially unstable, but tamed by the periodic inhibition induced by the LH, is exploited, via different readout maps (mimicking the MB output neurons), to serve a number of associations with other conditioning signals, coming from other parts of the brain. In that way the same structure can serve, at the same time different tasks concurrently. In our model we explicitly concentrated on decision making (classification), motor learning, sequence and sub-sequence learning, delayed matching to sample, attention, expectation, and others. Sequence learning could be further developed to implement an efficient capability of planning ahead, a key characteristics of cognitive systems. Our model represents the computational implementation of the concept of neural reuse in the insect brain: MBs are considered as the generators of a rich dynamics, controlled by sensory stimuli. Such dynamics is then shared and sub-divided, according to specific associations, and deployed for different concurrent tasks. We expect that the new view on the MBs will trigger inspection by neurobiological experiments and that the outcome will confirm this concept of re-use. Mutual benefit is expected from producing novel neurobiological details, and, at the same time, preparing more detailed simulations. The outcomes of the computational models could provide new ideas for the

design of specific experiments focussed on revealing new impressive capabilities of the insect brain.

The model described in chapter 5 takes only a small portion of the fly brain functions outlined in chapter 1. For example, at the end of chapter 1 it was underlined that, long-term autonomy will comprise additional interesting behaviours that will have to be fundamental components of the adaptive robot of the near future. One of these behaviours is novelty choice, a key-component of curiosity. This was recently addressed as a result of the interplay found between CX and MBs [16]. Currently, efforts are made to assess novel results from the biological side and to transfer them into efficient models which could contribute to build efficient autonomous machines.

In the eye of the authors, the insect brain represents one of the best places to identify the basic rules and find the solution to build a completely autonomous machine. The treasure of behavioural capabilities, so far identified in insects, is expected to further increase in the near future. Even complex behaviours that, judged from today's view are unlikely to be shown by insects, could be found, with suitable experimental design. One example is the discovery of the capability to solve the Morris water maze task in cockroaches, crickets and *Drosophila*, a task involving complex spatial working memory. Insects really are the model organisms of choice, able to inspire the design and realization of the most advanced all-terrain robots of the near future. This will require efforts from a multi-disciplinary perspective in order to achieve a solid advancement of science and technology.

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