Temporal and structural neural asymmetries in insects

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Neural asymmetries of the bilateral parts of the nervous system are found throughout the animal kingdom. The relative low complexity and experimental accessibility of the insect nervous system makes it well suited for studying the functions of neural asymmetries and their underlying mechanisms. Recent findings in insects reveal hardwired asymmetries in their peripheral and central nervous systems, which affect sensory perception, motor behaviours and cognitive-related tasks. Together, these findings underscore the tendency of the nervous system to segregate between the activities of its right and left sides either transiently or as permanent lateralized specializations.

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"The problem of the relation of right- and left-sidedness to the more general law of bilateral symmetry has not yet been studied with the method or comprehensiveness which it requires and which is now possible" (Hall and Hartwell, 1884)

Studying neural asymmetries in insects

Bilateral symmetry governs much of our neuroanatomy, but exceptions have fascinated scientists since the early days of modern brain studies (e.g. Ref. [1]). Yet, to date, we know little about the emergence of lateral brain specializations from the overall symmetric neuroarchitecture. A major breakthrough in addressing this issue came from the understanding that neural asymmetries are not unique to humans, but ubiquitous across the animal kingdom [2].

Insects are specifically noteworthy from this perspective. Their nervous system is relatively small and accessible, while their behaviour is complex but often traceable. Additionally, developments in genetics, specifically in — but not limited to [3] — *Drosophila melanogaster*, offer exceptional tools for deciphering and manipulating brain development and functions. Therefore, insects allow exploring neural asymmetries at different resolutions, from specific molecules and genes to the function of neurons, circuits and brain structures, and ultimately connecting those with behaviour. This review focuses on recent advancements in these directions.

Asymmetric activity in the nervous systems of insects

Insects are bilaterians. Anatomically, they exhibit, for the most part, anterior-posterior and dorsal-ventral asymmetries, whereas their left and right body sides are mirrored (for exceptions see, for example, mandibles: [4]; genitalia: [5]). The macroscale organization of their nervous system is similar: interconnected segmental ganglia, symmetrical on the lateral axis and asymmetrical along the longitudinal one.

Despite this general left-right symmetrical architecture, the function of the nervous system is often asymmetric. For example, sensory perception requires distinct activities of bilateral sensory centres in order to maintain information about asymmetric environmental cues (e.g. Ref. [6]), and turning behaviour requires distinct motor outputs to each side of the body [7]. These kinds of asymmetrical activities arise from symmetrical neuronal networks, capable of differentially activating bilateral parallel parts of the nervous system. Therefore, these asymmetries are transient and can interchange in a matter of milliseconds. However, some asymmetries take the form of consistent lateralized tendencies and specializations. For example, some animals show consistent biastowards turning left or right (e.g. Ref. [8]) and exhibit better performance in specific tasks when using a specific side (e.g. Ref. [9]). Such asymmetric behaviours indicate that within the general symmetrical anatomy of the nervous system, there might be some hardwired microanatomical and physiological deviations from symmetry.

In the current review we propose to look at both kinds of neural asymmetries — temporal and structural — as two extremes of one capacity: the propensity of the nervous system to segregate between the activities of its sides (see

Box 1). This propensity is fundamental for adaptive and effective behaviours of the individuals, and can both widen the behavioural repertoire of the organism (neatly demonstrated by Braitenberg vehicles [10]; see Figure 1a) and maximize its neuronal capacity (e.g. Ref. [11••]).

Putative sensory asymmetries

Segregation between the activities of the two sides of the nervous system is instrumental for screening an asymmetric environment by the bilateral symmetrical nervous system. In the olfactory system of *Drosophila*, for example, receptors from one antenna activate projection neurons (PNs) in both antennal lobes (ALs; [12]). When an odour is laterally presented to a fly, a 3 ms gap separates between the EPSPs generated in the ipsilateral and contralateral PNs. This gap is both necessary and sufficient for generating an appropriate turning response towards the odour [6]. Here, symmetrical sensory networks (the bilateral receptors–PNs connections) integrate and translate minimal asymmetrical activity into adaptive behaviour.

However, not all olfactory stimuli trigger the same activity in both ALs in *Drosophila*. For example, unilateral stimulation of the antennae with repellent odours activates both ALs equally, while attractants activate mainly the stimulated side [13]. Therefore, possibly, coding of sensory information utilizes differential activation of contralateral symmetrical networks for representing and processing stimuli of different values.

In addition to these temporary asymmetric activation patterns, functional differences between left and right parts of the nervous system have been showed to be at least partially hardwired along the sensory system. For example, the insect olfactory system exhibits a series of asymmetries. Few insect species have been shown to have asymmetrical distribution of olfactory sensilla between the left and right antennae ([14–17]; see also biased number of ommatidia in house-hunting ants; [18]). In the honey bees, in which the right antenna encompasses more olfactory sensilla and show higher responsiveness to sugar [19], the right antennal nerve also produces larger afferent signals in response to some odours [20]. In the brain itself, however, neither the anatomy of the ALs glomeruli, which the antennal nerve innervates [21], nor the strength of odour-driven activity at the level of the PNs were found to be asymmetrical [22]. Nevertheless, the inter-odour distances of odour-evoked neural activities in the right AL are larger than those in the left AL [22]. Therefore, when asymmetric odour responses are transferred via the sensory neurons to the antennal lobe, local interneurons probably play a role in reorganizing this asymmetry rather than directly streaming it centripetally. The higher inter-odour distance in the right AL also suggests that the right side has higher ability in discriminating odours [23]. Supporting this idea, bees

with only the right antenna intact are better in detecting a specific odour from a background than their counterparts with an intact left antenna only [22].

The visual system of *Drosophila* provides an example for the importance of micro-structural, persistent asymmetries for generating accurate responses to visual inputs. The dorsal cluster neurons (DCNs) connect the visual system of one hemisphere with either the medulla or lobula of the other side [24]. However, their exact innervation patterns show great variability between hemispheres and individuals [25]. Linneweber *et al.* succeeded in causally relating higher asymmetry of DCNs innervating the medulla to a better performance in orienting towards objects ([26••], Figure 1b). Here, the nervous system's ability to have side-specific differences in microanatomical structures optimizes individual behaviours.

Putative motor asymmetries

There are various examples of asymmetries in motor behaviours in insects that are not directly linked to sensory-driven behaviours. Often, these biases characterize only specific motor behaviours, as in antennae grooming (cockroaches: [27]), gap crossing (locusts: [28]) and use of antennae (ants: [29,30]). Yet, biases can also appear in more complicated social and mating behaviours (for review [31]). Potentially, motor behavioural asymmetries can arise from biases in the sensory perception, neuronal computation or motor output. Yet only a few studies investigated the neural asymmetries underlying biased motor behaviours.

To the best of our knowledge, the only example of persistent asymmetry in the motor output itself — in the absence of possible sensory asymmetries — was found in the control of legs in the locust (for transient asymmetries in this system, see Box 1). This was first reported by Chapple, who recorded directly from motor nerves innervating the locust legs, and found that one nerve was often more active than the other [32]. Knebel *et al.* further examined this phenomenon in isolated nervous system preparations, under different conditions, and found both individual and population level asymmetries in the motor output to the front legs [33•]. This finding indicates that asymmetries can be hardwired in the neuro-motor circuits, and not result from immediate sensory stimuli.

In respect to locomotor behaviours, many insects have shown idiosyncratic asymmetry in choosing between turning left and right when tested in a double choice maze (e.g. ants: [34]; 7-spot ladybird: [35]; bumblebees: [36] and crickets: [37••]; for review: [31]). In *Drosophila*, even though the turning bias of the entire population is not different than random, individuals show consistent turning biases, which are stable both over time and across different behavioural tasks [8,38]. Buchanan *et al.* reported that either silencing or hyperactivating a subset

Box 1 Differential activity in the control of legs: an example of bilateral flexible connections

The capacity to segregate between the activity of the two sides of the nervous system is a fundamental feature of neuronal networks, as the neural control of the legs exemplifies. Each of the three pairs of the insect legs is controlled by one of the three thoracic ganglia. These three interconnected ganglia can be deafferented easily, or even dissected out of the body cavity, and still maintain vital. Thus, investigation of the network in complete absence of sensory inputs is possible.

When this entire, interconnected, *in vitro* system is activated pharmacologically, synchronous rhythmic bursts of action potentials are generated in the motor nerves innervating the legs [55,56]. However, when only the metathoracic ganglion is activated, the pattern changes: the bursts within each side of the interconnected ganglia remain synchronized but the two sides burst in alternating fashion [56,57]. Interestingly, if the suboesophageal ganglion (one of the head ganglia, situated between the brain and the thoracic ganglia) is left intact to the metathoracic-activated ganglia chain, the whole system is bursting, once more, in synchrony [58].
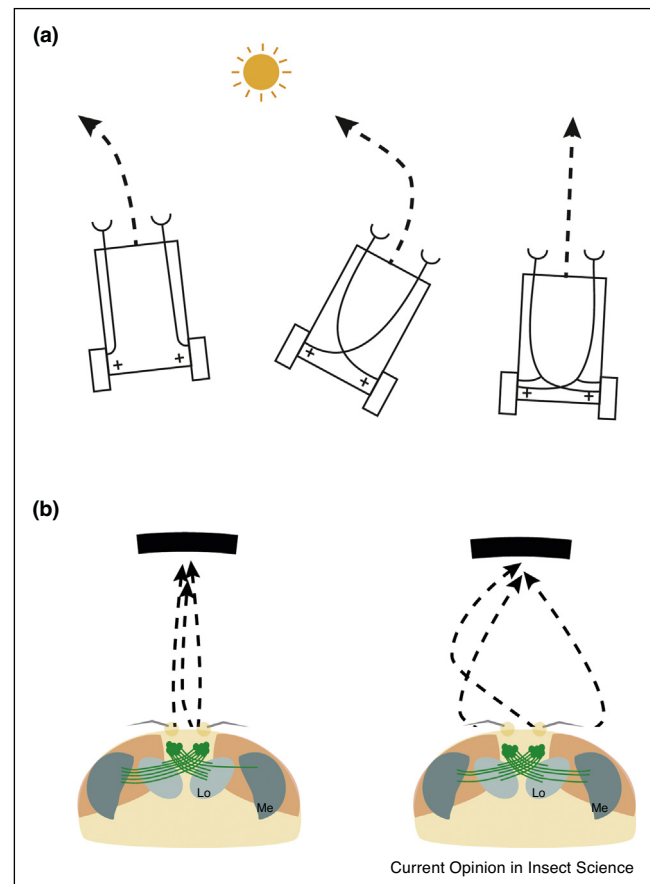
This neuronal network, therefore, brings evidence of the propensity of the nervous system to segregate its activity: the two lateral sides of the thoracic ganglia can act autonomously, yet the bilateral connections are flexible and can entrain them to act in temporal symmetry or asymmetry. This modular architecture, including the two sides of the thoracic ganglia and the suboesophageal ganglion, allows the various tasks insect legs are responsible for (e.g. walking, jumping, grooming and reaching for food), and require different degree of agreement between the legs.

Figure 1

Current Opinion in Insect Science

Bilateral wiring affects behaviours.
(a) Examples of Braitenberg vehicles that have different sensor-motor wiring. Simple modifications of the sensor-motor connectivity can result in different behaviours: vehicles with two autonomous and symmetric sensor-motor connections (left and centre) would either drive away or towards an asymmetric environmental sensory stimulus, whereas, equal interconnections between both sensors and motors would yield only straight driving, independent of the stimulus exact position. Modified after Braitenberg [10]. **(b)** Bilateral asymmetric wiring of the DCN cluster neurons in the medulla (optic lobe, see schematic wiring in green; Lo: lobula; Me: medulla) of *Drosophila* improves orientation towards an object (black bar). Modified after Takagi and Benton [59].

of neurons in the central complex (CX), increases the idiosyncratic biases of individuals [8]. Ayroles *et al.* found that the gene *Tenascin accessory*, which is related to the development of the CX, regulates the population level turning bias variation: when its expression was disturbed, the variability among individuals increased [39]. However, to the best of our knowledge, only one study was able to connect between asymmetry in the CX and the turning preference. Skutt-Kakaria *et al.* found that a subset of neurons, connecting the protocerebral bridge of the CX to the lateral accessory lobe, shows different synaptic pattern between hemispheres and individuals [37••]. Furthermore, the more synapses these neurons have in one hemisphere, the higher the probability of an animal to turn to this side. Additionally, by activating these neurons in one of the hemispheres, the turning behaviour could be manipulated [37••]. Together, these examples suggest that neural asymmetry in the connectivity of higher motor centres exists and plays a causal role in asymmetric motor behaviour.

Asymmetries in cognitive-related tasks

Few examples demonstrate asymmetric neural activity in higher brain functions, which might enable side-specialization of tasks and maximization of neuronal capacity [39].

The asymmetric body (AB) in the brain of *Drosophila* is a part of the central complex that was previously thought to reside in most individuals in only one side of the brain [40,41], but was recently shown to be bilateral with asymmetric size and innervation patterns [42]. Pascual *et al.* showed that *Drosophila* flies with an AB on one side (probably to be interpreted as the bigger one on the basis of Wolff and Rubin [42]), perform better in long-term memory tasks than the low percentage of flies that had symmetric structures [40]. Here, a relatively large

asymmetric neuroanatomical feature improves memory performance.

Many studies were dedicated to asymmetrical learning and memory in honey bees. A bee can learn to associate an odour with a sugar reward. After learning, the bee would extend its proboscis (proboscis extension response — PER) when it is stimulated by the odour, even in the absence of sugar [43]. Thus, a single antenna can be trained independently, but the learned response can be retrieved by stimulation of both antennae, with better performance in the trained one [44]. However, if each antenna is trained with contradicting associations, the responses to odours will be in accord with the learned associations, namely antenna-specific [44]. Therefore, learning can lead both to bilateral segregation or to information transfer (for a schematic model see Ref. [45]). Furthermore, the hypothesis of Sandoz *et al.* [45], according to which the mushroom bodies take part in this process was recently supported by electrophysiological experiments coupled with behavioural tests [46].

Several studies indicate that memory performance has side-specific properties. In particular, short-term memory tasks (up to 3 hours) are better performed with the right antenna [20,15,47,21] while performance of long-term memory tasks (3–24 hours) are better with the left one [9,47,48]. The same was found to be true for wood ants [11••]. Yet, some studies in bees report that even long-term memory is better when recalled with the right antenna [14]. Nevertheless, evidence for asymmetries during learning (before retrieval) was shown only in visual tasks [49] and not in odour tasks [22].

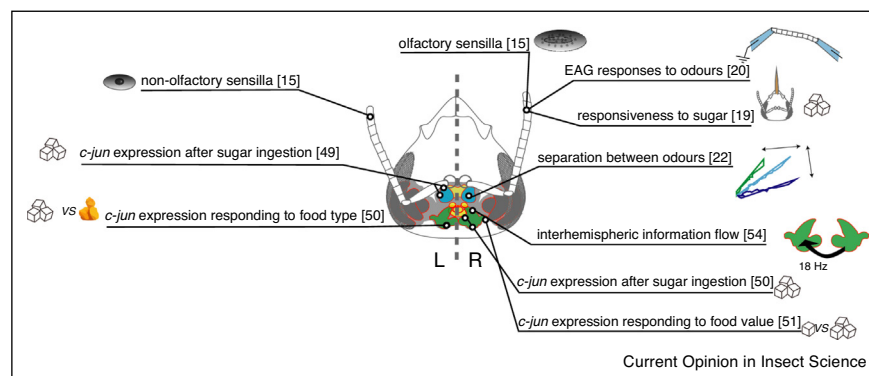Coupling these behavioural essays with neurobiological examinations shed some light on the cognitive-related biases: Various genes were shown to have enhanced expression on the right hemisphere, including learning-and-memory related genes [48]; The left and right hemispheres show different expression levels of *c-jun* (a gene that indicates enhanced neuronal activity) after receiving a food of different value [50,51], and different metabolic profile after proboscis extension response [52]; *Neurolgin* 1, a gene related to synapse formation, has a differential expression over time after either the left or right antenna are cut [53]; After a learning paradigm with only one antenna, the gene expression in the entire brain is higher for training with the right antenna [48]; During spontaneous spiking activity, 18 Hz oscillations (analogous to the alpha oscillations in humans) going from the right to the left mushroom body are stronger than vice versa, which might suggest a stronger flow of information in this direction [54]. See Figure 2 for neural asymmetries in the brain of untrained honey bee foragers that are potentially involved in biased learning and memory tasks.

Conclusion

The examples of neural asymmetries discussed lead to two major conclusions. First, neural asymmetries are spread in various aspects of neuronal activities. Second, they appear in different resolutions — from transient differential activity between sides to asymmetric neurons and neural structures. Moreover, as different as the examples might be, they all demonstrate the capacity of the nervous system to segregate between the activities of its bilateral symmetric sides.

We believe that in order to elucidate the phenomena of neural asymmetries as a whole — and not as an ever-growing list of examples — the field should concentrate on a double approach: understanding the benefits of asymmetry (see Box 2) along with the mechanisms that allow it. Computational modelling can produce predictions of the possible benefits of biased activity, and

Figure 2

olfactory sensilla [15]
non-olfactory sensilla [15]
EAG responses to odours [20]
c-jun expression after sugar ingestion [49]
responsiveness to sugar [19]
c-jun expression responding to food type [50]
separation between odours [22]
interhemispheric information flow [54]
c-jun expression after sugar ingestion [50]
c-jun expression responding to food value [51]
L R
18 Hz

Current Opinion in Insect Science

Neural asymmetries in honey bees.
Side-specific neural correlates of sensory tasks in naïve honey bee foragers (*Apis mellifera*) that might be involved in asymmetries of olfactory memory retrievals in bees.

Box 2 Benefits of neural asymmetries in insects

The benefits from breaking symmetry are various and can have very different nature. For example, one possible benefit is in foraging behaviour. Imagine a naïve insect, with no exploration strategy for gathering food. When this animal is foraging, aiming at bringing food back to its nest, it would benefit from exploring areas close to the nest site. Going mostly straight, with 50% turning probability to the right or left, would, on average, drive that animal to explore at distant locations. However, even a small bias in turning towards one side could enlarge the animal's probability to circle around the nest and find food in greater proximity (see similar model: [35]). Clearly, symmetry in this case would become a burden, while asymmetry — resulting from biased motor output to the legs — would make foraging more efficient.

Another example of a benefit, yet very different, is the asymmetric compartmentation of memory abilities. While much of the nervous system is dedicated to controlling paired (or when on the midline, symmetric) body parts, higher brain functions need not to be doubled [39]. Beyond the unnecessary and costly maintenance of the exact same brain structure on each side, having two independent memories, consolidated both on the left or right sides, can cause perplexity. In order to make them coherent each brain side could have different skills. This solution decreases unnecessary doubling of functions, might make better use of the limited neuronal tissue, and ultimately generate one coherent data base for the animal upon which its behaviour can be shaped ([39]; for evolutionary development of asymmetries in insects see Ref. [31]). In addition, also a side-segregated memory might be beneficial — for example, context-dependent memory is essential and the sides can be interpreted as different contexts [44,45].

Only a few evidence of asymmetric advantages were found in insects. For example, in *Drosophila*, an asymmetric DCNs arborization improves orienting behaviours [26**] whereas asymmetric AB size improves long-term memory [40]. Many of the presented examples lack supporting data about the biological possible advantages they introduce. We believe that in order to understand neural asymmetries in a broad biological context, providing evidence for possible advantages is essential.

genetic analyses coupled with functional recordings (electrophysiology, imaging, lesion and behavioural studies) could help unravelling the developmental, physiological and evolutionary mechanisms underlying the differential activity of the nervous system. Insects, for their relatively small nervous system and complex behaviour should be key models in adopting this approach. Here, by putting together various examples of neural asymmetries in insects, of different modalities and resolutions, we hope to push the research of this phenomenon forward as a field.

Conflict of interest statement
Nothing declared.

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Papers of particular interest, published within the period of review, have been highlighted as:

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- •• of outstanding interest

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