# Appendix B: Trait descriptions and criteria

## 1. Body Traits

The evolution of metazoan body plans involved at least six major steps (Nielsen, 2008). The first major step was the coalescing of multiple cells into a single functional unit or body in which nutrients could be exchanged between cells. The second through fourth steps marked major changes in multicellular tissue differentiation, organization and function, including the formation of an enclosed cavity for extracellular digestion of food, a distinct nervous system for processing sensory information and striated muscle for effecting behavior. Together, tissue traits are diagnostic of Eumetazoa, a monophyletic clade that includes all metazoan phyla except Porifera (sponges). The fifth step marked a major transition in body symmetry – from non-bilateral to the bilateral symmetry of metazoan animals collectively known as Bilateria (a metazoan subkingdom). The final step involved the formation of a ‘through’ gut incorporating both a mouth and anus, which together with a centralized nervous system and well-defined brain defines the Eubilateria (Nielsen, 2008; Nielsen, 2012; Nielsen et al., 2018), a monophyletic clade consisting of nearly all bilaterian phyla except a few (e.g., Nemertea and Platyhelminthes). The first four of the following body traits represent major novelties associated with steps 3 – 6, whereas the last two traits - paired appendages and flexible limbs - represent important de nova traits that led to increased flexibility, maneuverability and range of motion.

#### Neurons and nerve tissue (Step 3)

Cnidaria, Ctenophora and all bilaterian phyla possess distinct nerve tissue that consist of specialized cells (neurons) for rapid transmission of information from cell to cell (Nielsen, 2008). The development of nerve cells into a differentiated nervous system in these groups is furthermore driven by shared gene regulatory networks and transcription factors (Smarandache-Wellmann, 2016, see Appendix C). Neuron properties shared by both vertebrates and invertebrates include the (1) anatomical and functional differentiation (polarization) of neurons into input (dendrites) and output (axon terminal) regions, as well as an elongated transmission line (axon), (2) voltage-dependent sodium and potassium ion channels in the cell membrane that underlie information-bearing signals known as action potentials, (3) electrical or chemical transmission of information in the gap (synapse) between the output region (axon terminal) of one cell and the input region (dendritic surface) of the next, and (4) neurotransmitters types (Smarandache-Wellmann, 2016).

#### Mesoderm and striated muscle (Step 4)

The addition of a third (middle) germ layer, the mesoderm, to a diploblastic (ectoderm and endoderm only) condition is regarded as an important step in the evolution of metazoan animals (Burton, 2008) (Nielsen, 2008). For one thing, it facilitated greater specializations and differentiation of tissue systems, including the nervous system. As a result, far greater body plan and species diversity is associated with triploblastic bilaterians (~30 phyla, > 106 species) relative to diploblastic non-bilaterians (~ 4 phyla, ~3 x 105 species) (Burton, 2008).

In bilaterian species, mesoderm gives rise to striated muscle, characterized by alternating bands of thick and thin contractile filaments comprised of actin and myosin (Burton, 2008). There is some controversy as to the evolutionary origins of striated muscle and whether striated muscle evolved once in the common ancestor of cnidarians and bilaterians (Seipel & Schmid, 2005) or several times from a diploblastic ancestor without striated muscle (Burton, 2008; Steinmetz et al., 2012). Nevertheless, there is general agreement that all metazoan phyla except Porifera have striated muscle, whereas only bilaterian phyla have ‘true’ mesoderm.

#### Bilateral symmetry and associated traits (Step 5)

This primitive trait is shared by > 99% of all extant species (Finnerty et al., 2004; Hollo and Hovak, 2012) and is widely recognized as a key step in the evolution of metazoans as a whole (Nielsen, 2008; Erwin 2020) and of the brain and central nervous system, in particular (Nielsen, 2008, Manuel 2009). Whereas *cephalization* (concentration of neurons, a brain, and sensors on the head) at the anterior end of the body with a posterior nerve cord (deuterostomes) or cords (protostomes) is characteristic of bilaterians, distributed nerve nets and rings with sensors distributed around the body circumference are characteristic of animals with radial or biradial symmetry (e.g., cnidarians, ctenophores and echinoderms). Note that echinoderm larvae have bilateral symmetry and for this reason, Echinodermata is classified as a bilaterian phylum. Here, however, we classify according to the adult form (see Section 6C in main paper).

#### Through-gut (Step 6)

The evolution of a tubular gut made digestion more efficient and enabled further specializations of various parts of the digestive system (Nielsen, 2008; Nielsen, 2012; Nielsen et al., 2018). The through-gut design, with a mouth at one end and an anus at the other, likely co-evolved with other anterior-posterior differentiations of the body, including the differentiation of the nervous system into posterior (nerve cord/s) and anterior (brain) parts (Nielsen, 2012). Together, these traits, characteristic of Eubilaterians, were regarded by Nielsen (2008) and others (Seipel and Schmidt 2005) as an important step that enabled the evolution of bigger animals and more complex behaviors. A tubular gut is diagnostic of most eubilaterian phyla but absent in Porifera, Ctenophora and Cnidaria. However, the anus has been secondarily lost in some phyla, notably Brachiopoda and Platyhelminthes (Boyer et al., 1998; Dunn et al., 2008; Lartillot and Philippe, 2008).

#### Paired appendages and flexible limbs

Paired appendages are quite varied in form and function, and include the wings of insects, birds and bats, the flippers of aquatic mammals and the fins of fish and cuttlefish, the walking legs of euarthopods and vertebrates, the arms and hands of primates, and the arms and tentacles of cephalopod mollusks and echinoderms. The paired appendages of cephalopod mollusks are a little different from other animals in that they consist of a bilaterally symmetric structure, the arm crown, which consists of four pairs of prehensile arms with an additional pair of mobile cirri or tentacles (Nodl et al, 2016). Paired appendages can be broadly categorized into three functional groups in terms of their capacity for complex motions: (1) unjointed, relatively inflexible limbs with few degrees of freedom, (2) articulated (jointed) limbs, consisting of independently controlled, rigid segments that afford several degrees of freedom, and (3) highly flexible, unsegmented limbs with nearly infinite degrees of freedom. Unjointed limbs (lobopods and parapodia) with a small range of motion are found in three extant phyla: Onychophora, Tardigrada and Annelida. Interestingly, several families of highly mobile polychaete annelids possess compound or jointed setae at the tips of their parapodia (Merz and Edwards, 1998), but these are not innervated or controlled by muscles (Gustus and Cloney, 1973). Echinoderms have numerous, jointed ossicles along their arm rays making them fairly flexible, with those in brittle stars (Ophiuroidea) being far more flexible than those in starfish (Asteroidea)(Schwertmann et al, 2019). True jointed limbs are thus found in echinoderms, vertebrates and euarthropods, whereas unjointed but otherwise flexible limbs are found in cephalopod mollusks.

## 2. Motor Traits

Motor systems are used in a wide variety of behavioral contexts, including long- and short-range navigation to find food or suitable habitats, transient escape maneuvers from predators, food acquisition, prey capture and conspecific interactions, such as those involved in reproduction and agonistic interactions. In all of these and other behavioral contexts, dynamic sensorimotor processing in the brain and peripheral nervous system controls the timing, acceleration/speed/deceleration, and direction of body (and body part) movements, which represent the motor output of the brain. Motor traits focus on three categories of motor actions, all of which are broadly subsumed in a wide range of behaviors. The first five traits (mobility, 3D mobility, polarized locomotion, appendicular locomotion, and high-speed locomotion) all revolve around locomotion, which entails the movement of the entire body from one place to another, with multiple ways of achieving this (Table 1). The sixth trait, object manipulation, involves object-oriented, body-part movements, which entail the independent movement of limbs, mouth and other body parts towards objects of interest. Finally, the last trait, eye mobility, involves the independent movement of the eyes within the head to track items of interest and to stabilize the visual surround during locomotion. Some of the behavioral contexts and broader functions of these motor traits are discussed further in Section 5 (*Behavioral and cognitive* *trait*s).



#### Mobility

Mobility, as defined here, is synonymous with locomotion, and is simply the ability of animals to move from one location to another. Locomotor tracks in the fossil records indicate that there were large motile, cnidarian-like organisms on the seafloor as early as 565 mya (Liu et al., 2010; Chen et al., 2019)(Fig.4). Mobility thus marked an important transition from the largely sessile guilds of the early Ediacaran (~ 630 mya) to the first benthic fauna during later Ediacaran and early Cambrian periods (Butterfield, 2007; Schiffbauer et al., 2016). Mobility is so widely distributed that it is of little use in discriminating between CC and non-CC lineages, but it is included here because it is so fundamental to the evolution of brains (Arendt et al. 2015) and the embodied view of cognition (Clark, 1998; Engel et al., 2013; Pfieffer et al. 2007; 2014).

Mechanisms of locomotion, as Dickinson et al. (2000) so succinctly summarized, can be boiled down to “appendages that oscillate or bodies that undulate, pulse, or undergo peristaltic waves”. All of these involve the application of a force on the external environment (air, water or substrate) in order to accelerate the body in the opposite direction (Dickinson et al., 2000). Whereas ciliary mechanisms are reserved for slow crawling or swimming (Jekely, 2011), muscle-powered mechanisms are used for all types of locomotion (Zug 2020; Kuroda et al 2014), ranging from peristaltic waves for slow crawling to rapid body contractions for jet propulsion (Table 1). Many animals use more than one mechanism and/or mode of locomotion (Lock et al., 2014; Kuroda et al., 2014) (Table 1). Bees, for example, use leg oscillation to walk or run on a substrate, but wing oscillations to fly in the air. Octopi use jet propulsion for rapid swimming mid-water, but oscillation of flexible arms for walking on the sea floor. Primates use oscillating limbs for bipedal or quadrupedal locomotion on land, arboreal brachiation in the trees and swimming in bodies of water.

Most, but not all extant metazoans are mobile, using some form of locomotion to move around on a regular basis. Major exceptions include Porifera (sponges), which have mobile larvae but sessile adults, and the adults of several bilaterian taxa, which have adopted sessile or sedentary lifestyles. These include brachiopods, and some molluscan (e.g., bivalves), nemertean and annelid (e.g., Sedentaria) taxa. Within at least one CC (Mollusca) and non-CC (Annelida) phylum, highly mobile species tend to have more complex brains and eyes than those that are sedentary (Harley and Aspen 2018).

#### Three-dimensional mobility

Locomotion is seldom steady-state and the ability to maneuver by turning, accelerating or decelerating is essential (Jindrich and Quoa, 2009). Ideally, quantitative measures of the maneuverability and/or agility of animals (as defined by Jabstretsky et al., 2016) would be desirable for characterizing the ability of animals to maneuver in three dimensions. Unfortunately, these data are unavailable for a wide range of phyla. Instead, we use locomotion modes as a back door to maneuverability in three dimensions. That is, animals that swim in water, fly in the air, or swing or glide through the trees must negotiate a three-dimensional world, being free to move in all directions, arguably a more spatially complex task than that faced by animals that are substrate-bound. Animals that walk, crawl or run on the substrate may indeed negotiate three-dimensional surfaces (e.g., crawl up a tree), but they do not have the same degree of freedom In the vertical body axis as animals suspended in air or water. That is, they cannot easily lift themselves off or bore into the substrate that supports them.

Fish, dolphins and cuttlefish all have independently evolved paired fins that increase their ability to maneuver (brake and steer) in their three-dimensional world (Jastrebsky et al., 2016). Aquatic animals that are pelagic and swim on a regular basis are found in 7 lineages (Ctenophora, Cnidaria, Annelida, Echinodermata, Vertebrata, Cephalopoda (mollusks), and, Euarthropoda). However, non-bilateral symmetries and the absence of limbs severely restrict maneuverability in ctenophores and cnidarians, leaving only 5 lineages with animals that likely have any degree of 3D maneuverability. Flight has evolved in euarthropods (insects only) and in vertebrates (in Pterosaurs, birds and bats). As the simplest form of flying, gliding has evolved numerous times in different vertebrate groups, including amphibians, reptiles, mammals (Dudley et al., 2007; Bahlman et al., 2013), and in one molluscan family - the ‘flying squid’ (Ommastrephidae) (Silvia et al., 2004; Murmatsu et al. 2013). Arboreal brachiation, an object-oriented directed task that involves grasping of tree limbs by hands and digits and swinging from branch to branch using alternate arms, is limited to primates (Chordata) (Polet and Bertram, 2021).

#### Polarized locomotion

Bilaterally symmetric animals move in a polarized (headfirst) direction relative to the anterior-posterior body axis, while also maintaining a consistent body orientation with respect to gravity (dorsal side up, ventral side down). Absent a head, radially and biradially symmetrical animals do not technically exhibit headfirst locomotion, but different types of polarized locomotion do exist in these groups. Cnidarians and ctenophores often lead with either their oral (ctenophores) or aboral (cnidarians) side (Costello and Collin, 1995; Haddock, 2007). In addition, brittle stars (echinoderms) move in the direction of a temporarily selected ‘lead’ arm, but the direction changes frequently and without apparent preference for which arm takes the lead (Tomholt et al., 2020). For these reasons, polarized locomotion is attributed to ctenophores, cnidarians and all mobile bilaterians except echinoderms.

#### Appendicular locomotion

Muscle-powered mechanisms for locomotion can be broadly grouped into axial (contraction of body wall muscles) and appendicular (muscle-powered appendage oscillation) (Table 1). Of these, appendicular locomotion is the most versatile, being used in different forms of terrestrial (walking, running, jumping), fossorial (burrowing), aquatic (swimming) and aerial (flying, arboreal brachiation) locomotion in both vertebrates and invertebrates. It is also among the fastest forms of locomotion (Table 1). Appendicular locomotion is found in all seven lineages that possess paired appendages: Annelida, Onychophora, Tardigrada, Euarthropoda, cephalopod mollusks, Echinodermata and Verebrata (see also *Paired appendages and flexible limbs)*

#### High speed locomotion

High speed locomotion has several advantages, including improved abilities to (1) escape predators, (2) pursue and capture prey, and (3) cover more territory in shorter periods of time when searching for resources. Locomotion speeds in extant species range from a fraction of a mm/s in small swimming or crawling animals like nematodes and tardigrades to tens of m/s in larger running, swimming or flying animals, including fish (e.g., sailfish and marlin), squid, aquatic mammals (dolphins and whales), terrestrial mammals (e.g., cheetahs, wildebeest) and birds (hummingbirds, peregrine falcons) (Table 1). Amazingly, many small insects also run or fly in the m/s range (Table 1). The capacity for high-speed locomotion, defined as >= 1 m/s, involves either jet propulsion or appendicular mechanisms and has evolved independently in four lineages: Cnidaria, Vertebrata, cephalopod mollusks and Euarthropoda.

#### Object manipulation

Like three-dimensional mobility, object manipulation exemplifies spatially complex, sensorimotor skills (Trestman, 2013). Object manipulation typically relies on flexible appendages, which do the grasping and positioning of the object. However, other controllable body parts (e.g., mouthparts such as bird beaks) are also used (Sugasawa et al., 2021). Mechanisms that do not involve spatially complex, sensory-guided, goal-directed actions towards an object of interest are excluded from this category. These include the selective sorting of food particles by size in marine filter feeders (Kuzmina and Malakov, 2007; Bezares-Calderon et al. 2020) and the reflex by which jellyfish retract tentacles bearing food toward their mouths (Satterlie, 2015).

Object manipulation spans a wide range of sensorimotor abilities and behavioral functions. Food manipulation by mouth parts or surrounding appendages is a crude form of object manipulation by animals in some non-CC phyla, including sea cucumbers and brittle stars (Echinodermata) (Dearborn et al., 1981; DíazBalzac et al., 2010; Hamel & Mercier, 1998), velvet worms (Onychophora) (Barquero-Gonzalez et al 2019), and polychaete and crayfish worms (Annelida) (Gale and Proctor, 2011; Mills and Mortimer, 2019). Other annelids, such as earthworms, manipulate non-food items, in this case leaves, to line their burrows (see Darwin’s (1881) classic experiments reviewed in Korb and Salewski, 2011). Many animals, particularly in the three CC lineages, also manipulate raw materials to construct all sorts of housing (e.g., bird nests) and other structures (e.g., mating bowers, spider webs) (see *Cognitive and behavioral* *traits, Construction behaviors).* Object-oriented play is another fascinating example of object manipulation by nearly all vertebrate classes (Burghardt et al, 2014), but also octopi (Mather, 2022) and bumblebees (Galpayage et al, 2022).

Tool use and manufacture represent a more narrowly (and somewhat inconsistently) defined form of object manipulation (Hansell and Ruxton,2008; St Amant and Horton, 2008; Bentley-Conduit and Smith, 2010), often considered to be more advanced and cognitively sophisticated than other forms of object manipulation. However, where tool use falls on the continuum of cognitive abilities is irrelevant to its classification as a form of object manipulation. Animals use tools for different behavioral functions including (1) food procurement, (2) maintenance of the body, (3) mate attraction, (4) nest construction, (5) predator defense and (6) conspecific aggression (see Bentley-Conduit and Smith, 2010 for a review). Examples of tool use in vertebrates include New Caledonian crows crafting hooks and using them to extract hard-to-reach grubs (Hunt 1996), chimpanzees using stone anvils to crack nuts (Sakura and Matsuzawa, 1991), and tuskfish using stone anvils to crack bivalve shells (Jones and Brown, 2011; Pryor and Milton, 2019). Cephalopods demonstrate a number of tool use behaviors in nature, including using water ejected from their mantles as a tool to move sand or attract the attention of humans (Mather 2022). A unique tool use behavior has been reported in land-snails which, when turned upside down, can pass a stone up their body to use as a counterbalance in order to right themselves (Weldon and Hoffman 1975). Tool use is less frequently documented in arthropods, but several ant species use absorbent objects, like paper or strings, to transport liquid food (Morrill, 1972; Barber et al., 1989). All in all, examples of object manipulation, including tool use, can be documented for the three CC lineages plus three other non-CC phyla.

#### Eye mobility and compensatory eye movements

The primary function of mobile eyes is to prevent image blur when animals move (Walls, 1962: Land, 2012;2019). As Walls (1962) so aptly put it, “the original function of eye muscles was not really to move the eye but rather to hold it still with respect to the environment”. According to Land (2019), all animals with good vision (i.e., high resolution eyes) have very similar strategies for accomplishing this. They use compensatory eye movements to reflexively oppose the visual effects of turning the head or body (the vestibulo-ocular reflex, see Appendix B: *Sensory traits*). Similarly, the optokinetic reflex opposes the effect of optic flow (the apparent motion of the surrounding visual field when animals move or are passively transported via wind or water currents (optokinetic reflexes)(Walls, 1962; Budelmann, 1988; Mellon, 1977; Strausfeld et al., 2016; Daly et al., 2018). Optic flow also induces locomotor (swimming, flying, walking) reflexes (the optomotor reflex) to maintain visual stability (Rock and Smith, 1986; Land, 2019). All of these compensatory movements rely on inputs from body motion sensors (see *Sensory traits, Body motion senses*).

 The ability to move the eyes independently of the head and body also has potential advantages for the processing of visual information. It can (1) increase the volume of visual space that can be scanned and inspected (MacIver and Findlay, 2021), (2) generate dynamic, spatiotemporal information as a form of active sensing, (3) allow animals to track moving targets, (4) center targets of interest on areas of the retina that have high spatial resolution (e.g., foveas) and (5) provide all of these benefits while the animal remains stationary, thus minimizing whole-body motion cues that might give away the animal’s own presence.

Extraocular muscles control the motion of the optic vesicle (eyeball) in the head of vertebrates and cephalopod mollusks (Budelmann and Young, 1984; Budelmann, 1988; Land 2012), but in some euarthropods (spiders), there is a dedicated set of muscles that move just the retina behind the fixed lenses of their two, forward-looking principal eyes. Eye motion in other euarthropods, such as crustaceans, is controlled by eyestalks, which consist of three fused appendicular segments with the most distal segment bearing the compound eyes (Strausfeld et al., 2016). Multiple muscles control the coordinated movements of each eyestalk to both visual and body motion stimuli (Mellon, 1977; Strausfeld et al., 2016). Fossils with well-preserved eyestalks and optic centers indicate that stem-group arthropods used their mobile eyes for visual stabilization and active sensing of prey as early as 518 mya (Vannier et al., 2009; Strausfeld et al., 2016), whereas the first vertebrates (fishes) likely acquired this ability by at least 450 mya, perhaps even earlier (Land, 2012). Some alciopids (polychaete annelids) also have telescopic eyes that are mobile (Fernandez-Alamos and Theunes, 1999). To the best of our knowledge, there is no evidence for mobile eyes outside the three CC lineages and some polychaete annelids, all of which additionally possess high-resolution eyes and laminated visual regions (see S*ensory traits*, *High- and low-resolution vision and Brain traits, Laminated visual regions*)

## 3. Sensory Traits

If acquiring, processing, valuing, and acting on information is at the core of cognition (Shettleworth, 2010; Lyon et al., 2021), then it stands to reason that cognition would not be possible without the senses to acquire information in the first place. Interoceptors, such as body motion sensors and various muscle and joint proprioceptors, provide information on body motion, posture and position with respect to gravity, whereas exteroceptors (vision, olfaction, tactile, flow sensors) provide information on moving or stationary features of the surrounding environment, including how these appear to change as an animal moves past them. Here we focus primarily on exteroceptors and their capacities for distal sensing, noted for its importance to cognition (Llinas, 2002; Trestman, 2013, Jablonka and Ginsberg, 2021). Body motion senses are also included, because they often play a role in sound/vibration detection and spatial cognition (Markl, 2012; Gallistel and Matzel 2013). Furthermore, body motion sensors play an important role in being able to tell the difference between sensory stimulation that arises from an animal’s own actions (sensory reafference) vs that arising from ‘other’ external sources (sensory exafference). As such, they may contribute to a nascent sense of self (body awareness) (Montgomery and Bodznick, 2016). The following eight sensory traits were included in the analysis, one of which represents (1) a combination of two or more senses that afford multimodal sensing abilities, and the rest of which represent individual sensory channels, including (2) olfactory, (3) auditory/vibration, and (4) flow senses. Visual senses are subdivided into (5) low- and (6) high-resolution categories and body-motion senses were likewise divided into sensors that detect (7) translational and (8) rotational motions.

#### Distal and multimodal sensing

Distal sensing has been proposed by many as being important to the evolution of sophisticated cognitive abilities (Llinas, 2002; Trestman, 2013; Feinberg and Mallot, 2013;2018;2019;2020). There are two ways in which distant stimulus sources can be detected, one active and one passive. Passive mechanisms of detection rely on the long-distance propagation of signals (e.g., light, sound, odor, substrate vibrations) from distant sources through a medium (air, water or substrate) to sensors housed on the head or body. Active strategies take three different forms: (1) self-production of propagated signals (e.g., high frequency sounds, electric fields) to probe distant locations, as in echolocation by dolphins and bats (Au and Simmons, 2007) or active electrolocation in fish (Nelson and MacIver, 2006), (2) the use of elongated appendages with chemo and/or tactile sensors (e.g., cockroach antennae or antenniform ‘legs’ of whip spiders) to probe locations beyond the body core (Mongeau et al 2013; Bingman et al., 2017; Segovia et al. 2020), and (3) controlled body movement to create dynamic cues that depend on changes in the sensory input over time (e.g., optic flow, motion parallax cues about distance) (Horridge 1986; Kral, 2003; Schroeder et al., 2010).

 In the absence of direct body or appendage contact with a stimulus source, four sensory modalities are capable of distal sensing: olfactory, visual, auditory and to a lesser degree, flow-sensing. Using the criteria outlined below for each modality, we determined that all 17 lineages/phyla possessed at least one form of distal sensing - even Porifera, for which there is a putative form of flow-sensing in some species (Ludeman et al., 2014). Multimodal sensing, defined as a minimum of two distal senses, is present in at least 14 lineages, including all three CC lineages.

#### Olfactory senses

By all accounts, the ability to detect different chemicals is an ancient and broadly distributed sensory ability (Hildebrand, 1995; Dusenbery 1992; Ache and Young, 2005). Olfaction is defined as the detection of air- or water-borne chemical stimuli from a distant source, as opposed to other forms of chemoreception (e.g., gustation or taste) requiring direct contact with the source. For the three CC lineages, the demarcation between olfaction and contact chemoreception is clear and is based on multiple lines of evidence for a distinct olfactory modality, including (1) odor-guided behaviors to distant food and other odor sources (DeBose and Nevitt, 2008; Carde and Willis, 2008; Kamio and Derby, 2017; Scaros et al., 2018; Zjacic and Scholz 2022), (2) sense organs dedicated to olfaction (nasal cavities in vertebrates, feathery or hairy antennae in euarthropods, rhinophores and olfactory pits in mollusks)(Symonds et al., 2011; Harzsch and Krieger, 2018; Scaros et al. 2018), (3) dedicated 1st order processing centers in the brain (olfactory bulbs in vertebrates, olfactory lobes in euarthropods and mollusks) (see *Brain Traits*), and (4) distinct odorant binding and odor receptor proteins (Hildebrand, 1995; Eisthen, 2002; Kamio and Derby, 2017). Many, if not all lines of evidence also support the presence of olfaction in Nematodes (Eisthen, 2002; Zaitseva, 2016; Rengarajan and Hallem, 2016).

Unfortunately, the distinction between olfaction and contact chemoreception in non-CC phyla is less clear for several reasons, including (1) no clearly identified sense organ or brain structure dedicated to olfaction, (2) no universal genetic marker of odor receptors (Bargmann 2006; Eyun et al., 2017; Vizueta et al., 2020), and (3) the use of contact chemoreceptors by aquatic organisms (e.g. taste buds in catfish) (Kamio and Derby, 2017) to detect water soluble chemicals from a distance. In cases like these where the lines are blurred, we used at least one of four lines of evidence (behavioral, sensory, brain processing areas, or receptor proteins, see list above) to support an olfactory sense in seven additional non-CC phyla: Cnidaria, Echinodermata, Hemichordata, Annelida, Platyhelminthes, Bryzoa and Onycophora.

#### Auditory and vibration senses

Audition is defined here as the capacity to detect propagated sound pressure waves in an elastic medium (air or water) from a distant source. Vibration detection is similar in being the capacity to detect either the local particle oscillations integral to a propagated sound pressure wave or the mechanical disturbances propagated through an inelastic solid medium (substrate vibrations).

Mechanisms for detecting sound and vibrations have evolved in all three CC lineages and at least five non-CC phyla. Auditory organs typically operate in one of three ways, as (1) pressure transducers (most vertebrate ears), (2) pressure-gradient receivers (e.g., tympanal organs in amphibians and chordotonal organs in insects), or (3) vibration detectors that respond to the local particle oscillations in a traveling sound wave. Vibration detectors, likely the most primitive mode of hearing, include the antennal ears of insects (Albert and Kozlov, 2016), the otolithic organs of fish (Popper and Coombs, 1980) and the statocyst organs of many aquatic invertebrates, including mollusks, annelids, cnidarians, ctenophores, platyhelminths and nemerteans (Budelmann, 1988. 1992, 1994; Budelmann et al, 1984, Packard et al., 1990; Markl 2012).

Otolithic and statocyst organs also function as gravistatic and body-motion sensors (see *Body motion senses*). As a general rule, vibration detectors respond over shorter distances and to lower sound/vibration frequencies than pressure or pressure-gradient receivers. As with olfaction, there are multiple lines of evidence in support of auditory capabilities in the three CC lineages, including behavioral evidence of sound detection and communication and distinct auditory sense organs and neural pathways in the brain (Popper and Coombs, 1980; Packard et al, 1990, Hoy and Fay, 2012; Popper and Fay, 2012; Albert et al, 2016; Budelmann, 1995). The evidence for non-CC lineages is less clear, especially in aquatic invertebrates that have statocyst organs with potential dual functions in audition and body-motion detection and where the distinction between sound and vibration detection is less clear (Budelmann 1992). An auditory function of statocysts in cephalopod mollusks and cnidarians has received strong experimental evidence (Williamson, 1988; Kaifu et al, 2011; Sole et al. 2016, Jones et al., 2020), but in cases where confirmation is lacking, we made the simplifying assumption that statocysts, if present, had three potential functions - sound, vibration and body-motion detection.

#### Flow senses

Flow sensors that detect air or water currents relative to the skin surface can also detect the local flow from a sound-generating source (Braun and Coombs, 2000; Coombs, 2023), as well as flows produced by animal (or body part) movements through the air or water medium. Because local flows attenuate very rapidly with distance from the source, distal sensing capabilities are normally very short range (Kalmijn 1989). However, flow sensors also detect on-going, non-attenuating abiotic flows (e.g., wind, river currents) and this ability is often a vital component of the multisensory strategy used by many animals to track air or water-borne odor plumes from a distant source (reviewed in Carde and Willis 2008).

Flow sensors generally consist of superficially located, mechanosensitive hair-like structures (e.g. hair cells in the lateral line system of fish and amphibians or filiform hairs in insects) that are viscously coupled to the surrounding air or water. Flow sensors like these are found in all three CC lineages, as well as several non-CC phyla, including sponges (Ludeman et al., 2014) and annelids (see Bleckmann et al., 2014 for comprehensive coverage of flow sensing). Flow sensors are conspicuously absent in microscopic animals, such as rotifers and tardigrades. This is because the entire animal, being of such small size, is viscously coupled to and thus, moves with the surrounding medium (air or water).

#### Low- and high-resolution eyes

Vision is arguably the ultimate distal sense, providing animals with detailed spatial information about the world beyond them when conditions allow it (i.e., ample light, clear line of sight etc.). But not all photoreceptive organs are capable of forming spatial images. For example, the simplest of photoreceptive organs consist of relatively unspecialized cells that can detect temporal changes in ambient light intensity or the general direction of light, but not simultaneous spatial differences in ambient light intensity to form images of discrete entities from afar (Nilsson, 2009;2013).

The ability to form images relies on accessory structures, such as lenses, or other strategies for focusing and/or redirecting incident light onto photoreceptor arrays such that each photoreceptor receives light from a different point or direction in space (Land 2012; Nilsson 2013). Many invertebrate phyla have simple, single lens eyes, whereas vertebrates, cephalopods and at least one annelid (Hermans and Eakin, 1974) have more complex, single lens eyes with accessory features, such as a muscular iris for controlling the amount of light entering through the pupil. In contrast, euarthropods, most notably insects and crustaceans, are known for their multiple lens (compound) eyes (Arendt and Wittbot, 2001). Regardless of type, lenses have evolved multiple times in six lineages: Cnidaria, Cephalopod mollusks, Annelida, Vertebrata, Euarthropoda, and Onychophora (Land and Fernald, 1992), whereas other strategies for forming images can be found in another six non-CC phyla: Hemichordata, Echinodermata, Platyhelminthes, Nemertea, Tardigrada and Nematoda (Nilsson, 2013). Image-forming eyes of one form or another are thus present in 13 lineages.

Not all image-forming eyes are functionally the same, however, and are particularly diverse among invertebrates (Fernald, 2004; Purschke 2005). Lens-less strategies produce low resolution images, as do many lenses if, for example, the focusing power of the lens is too weak, as is the case for single lens eyes in Cnidaria and many insects and non-cephalopod mollusks (Nilsson et al, 2005, Nilsson, 2013). Based on optical and other features, image-forming eyes have thus been divided into low- and high-resolution classes (Nilsson, 2009; 2013)(see Table 2 in the main paper). Low resolution vision differs from high resolution vision in that it does not enable detection of and discrimination between small objects (Nilsson, 2022). A phylogenetic distribution of distinguishing features indicates that low-resolution eyes evolved several times independently - in both radially symmetric cnidarians and in many bilaterian lineages, including vertebrates and several invertebrate phyla (Nilsson, 2013). High-resolution eyes, on the other hand, appear to have evolved only four times, once in each of the three CC lineages - in vertebrates, cephalopod mollusks and euarthropods (Nilsson, 2009;2013), but also in some polychaete annelids (Hermans and Eakin, 1974; Randel and Jekely, 2016). Image-forming eyes of any kind are conspicuously absent in Porifera, Ctenophora, Bryozoa and Brachiopoda (Nilsson, 2013).

#### Body motion senses: translational and rotational sensors

Body-motion senses are perhaps best understood in vertebrates, where the semi-circular canals and otolithic organs associated with the inner ear in the head are collectively known as the vestibular system (Angelaki and Cullen, 2008). The semi-circular canals respond to angular accelerations of the head, whereas the otolithic organs respond to linear accelerations. The spatial orientation of the canals, otoliths and directionally sensitive receptor cells (hair cells) shape the best sensitivities of receptor cells to three rotational (pitch, roll and yaw) and translational (fore/aft, up/down, left/right) dimensions. Translational and rotational submodalities work together with vision and various proprioceptors to measure body orientation and motion in three-dimensional space and with respect to gravity (Angelaki and Cullen, 2008; Angelaki et al, 2009). Furthermore, they play a critical role in maintaining visuospatial and postural (orientational) constancy so that the visual surround does not appear to move and postures are not destabilized every time the head moves (Angelaki et al. 2009; Hitier et al., 2014). In this regard, the vestibulo-oculomotor system in vertebrates shows remarkable convergence with a very similar system in cephalopod mollusks (Budelmann and Young, 1984; Budelmann, 1988) to mediate compensatory eye movements (= vestibulo-ocular reflex) in order to preserve visuospatial constancy (see also *Mobile eyes*).

The use of body motion sensors to orient with respect to gravity has evolved several times in all three CC lineages, as well as in five non-CC phyla (Ctenophora, Cnidaria, Echinodermata, Platyhelminthes and Annelida) (Buddelmann, 1988; Markl 2012). The most common gravistatic organ is a fluid filled sac with one (statolith or otolith) or more (statoconia or otoconia) high density particles, which lag behind the accelerating tissues due to their greater inertia, thus stimulating the underlying, directionally sensitive mechanoreceptors. In addition to the otolithic organs of vertebrates, statocyst organs are found in several invertebrate phyla, mostly aquatic, where they often serve dual auditory and gravistatic functions (see *Auditory and vibration senses*). In decapod crustaceans and cephalopod mollusks, statocyst organs are organized at right angles to each other, similar to the organization of otoliths (utricle, saccule and lagena) of primitive vertebrates (fish) (Budelmann, 1988).

In addition to statocyst and otolith organs, which operate on the principle of inertia by responding to linear accelerations, some animal groups use different mechanisms for maintaining an upright posture. Insects rely on air-filled buoyancy detectors (aquatic insects) and joint proprioceptors (terrestrial invertebrates) (Markl, 2012). Many aquatic animals, both vertebrate and invertebrate, also make use of photoreceptors to keep the dorsal body surface oriented upwards, towards the downwelling light – the so-called dorsal light reflex (Preuss and Budelmann, 1995; Markl 2012; Jellies, 2014).

Sensors capable of detecting rotational accelerations appear to be limited to vertebrates (Chordata), decapod crustaceans and flying insects (Eaurthropoda) and cephalopod mollusks (Budelmann and Young, 1984; Budelmann 1988). Flying insects use structures at the base of their wings called halteres for detecting body rotation (Markl, 2012), whereas rotational sensors in aquatic invertebrates take the form of fluid-filled semicircular canals (Budelmann, 1988), as in vertebrates. Among cephalopod mollusks, octopi have particularly complex rotational sensors with adaptations for dual dynamic ranges, one for slow accelerations, presumably for use when crawling on the seafloor and the other for fast accelerations for use during rapid, jet-propelled movements (Budelmann 1988). In summary, it appears that sensors for detecting translational motions of the body (e.g., statocysts and otolith organs) in at least one or two dimensions are widespread, whereas only CC lineages have sensors capable of detecting both rotational (semi-circular canals and halteres) and translational (statocysts and otolithic organs) motions in three dimensions.

## 4. Brain Traits

Brains in CC lineages are anatomically and functionally differentiated into distinct regions or structures (Appendix B). Here we adopt the term *structured (vs unstructured)* fromHeuer et al. (2010) as our first brain trait to discriminate between lineages that do and do not have at least some evidence of brain differentiation into recognizable structures (but see *Pitfalls, gaps and future directions* in main paper). Our remaining brain traits are based on easily recognized and broadly defined brain regions that can be identified across all three CC lineages(see Appendix A). These include first-order processing areas with direct sensory inputs, most notably olfactory (trait 2) and visual (traits 3 and 4) regions. Visual regions of the brain are divided into two trait categories: those that process inputs from all manner of photosensors, whether they are non-imaging, low- or high - resolution eyes (1st order visual regions, trait 3) and those that are specialized for processing inputs from high-resolution eyes, characterized by distinct laminated and retinotopic organizations (laminated visual regions, trait 4). All three CC lineages also have learning and memory structures (trait 5), multisensory integration areas (trait 6) and motor hierarchies (trait 7) that consist of low-order motor regions for action execution, as well as mid- and high-order, multisensory integration, association, and motor control areas involved in executive control of behavior (see Appendix C). The final brain trait is a neural architecture with distinctive features (e.g., numerous, densely packed, small-bodied cells that give rise to thin, parallel fibers) that are commonly found in different brain regions in all three CC lineages (Farris, 2011, Beckers et al., 2022, Messenger, 1983; Shigeno et al., 2018) In the vertebrate cerebellum and some first-order sensory regions, these highly ordered structures function as *adaptive filters*, which, amongst other things, ‘learn’ to predict the sensory inputs expected from the animal’s own self-generated movements in order to distinguish them from world-generated movements (Montgomery and Bodznick, 1994; 2016). Six lineages (Porifera, Ctenophora, Cnidaria, Echinodermata, Hemichordata and Brachiopoda) are automatically assumed to lack these traits because animals in these groups lack cephalization and brains.

#### Structured brains

A structured brain is one that exhibits regional differentiation of the brain into recognizable structures, as identified for CC lineages in each animal grouping (see Fig 3, main paper and Appendix A). Brain structures can be thought of as an outward, more visible sign of functional modularity and complexity (Leise, 1990; Shih et al, 2015). Evidence for at least one of the five brain structures (or homologous regions) common to CC lineages was the criterion used for determining the absence or presence of structured brains in non-CC phyla. For deuterostomes, this was one of the five identifiable structures of the vertebrate brain (e.g., cerebellum, cerebral hemispheres etc.), whereas for protostomes, it was evidence of structures like mushroom bodies or central body complexes (see Fig. 3, Table 2 in Appendix A). Based on this criterion, five non-CC phyla were identified as having structured brains: Platyhelminthes, Annelida, Tardigrada, Onychophora and Nemertea (see Appendix A).

#### 1st order olfactory regions

Animals in all three CC lineages, as well as several non-CC phyla, have brain regions dedicated to the processing of primary inputs from olfactory sense organs. Furthermore, in euarthropods and vertebrates, this region is characterized by distinct spherical subunits called glomeruli. Among pancrustaceans (insects and crustacea), there can be between 50 - 170 of these subunits (Sombke et al, 2011), which are thought to be the basis of a ‘chemotopic map’ (Table 2 in Appendix A) for segregating odors into different functional categories, especially as they relate to behaviors (Ignell and Hansson, 2004; Bargman, 2006; Derby and Weissburg, 2014). The same is true for vertebrates, where in teleost fish, odors are segregated into behaviorally relevant categories, such as food odors and sex pheromones (Hamdani and Doving, 2007). Olfactory lobes and glomeruli are broadly distributed in both euarthropods and vertebrates and are also found in at least two non-CC phyla (Nematoda and Onychophora)(Schurmann, 1995; Eisthen, 2002). Mollusks have relatively small olfactory lobes (Young, 1971)(see Fig. 3C in main paper) without much, if any glomerular infrastructure (Cummins and Wyeth, 2014; Scaros et al., 2018). In any event, an anatomically distinct region that receives primary olfactory inputs, with or without internal glomeruli, is the criterion used here for mapping the taxonomic distribution of 1st order olfactory regions.

#### 1st order visual regions

In vertebrates, the 1st order processing stage of visual inputs is the retina, which develops as an out pocket (optic vesicle) of the prosencephalon (Chow and Lang, 2001), just as 1st order regions (optic lobes) of euarthropods and mollusks develop as extensions of the protocerebrum and supraoesphageal mass, respectively (Strausfeld, 2005; Young, 1971). The vertebrate retina and optic lobes of cephalopod mollusks and euarthropods receive visual inputs from high-resolution eyes (see *Low- and high-resolution eyes*). Nautilus is an exception among cephalopod mollusks in having lens-less (pinhole) eyes that are of low resolution (Nilsson, 2013) (see *Low- and high-resolution eyes*).

Euarthropods and animals in other invertebrate phyla have additional, low-resolution eyes (some with single lenses) called, called by various names, often median ocelli (see *Low- and high-resolution eyes*; Warrant et al, 2006). The sensory afferents from these eyes project to a ‘median eye center’ in the protocerebrum that is either bilaterally paired or medially fused (Harzsch et al., 2005). The median eye center, which goes by various names in different taxa (e.g. ‘ocellar’ ganglia in Onychophora) (Harzsch et al,, 2005; Mayer, 2006), is much smaller and far less differentiated than its optic lobe counterpart (Harzsch et al., 2005; Mayer, 2006, Strausfeld et al., 2006). For the purpose of assigning 1st order visual regions to different phyla, we use a liberal criterion to include visual regions that receive inputs from either low- or high-resolution, median or lateral eyes. However, retinotopically-mapped visual regions with nested optic neuropils (lamina) receiving inputs from lateral eyes are reportedly distinct from those associated with median ocelli (Strausfeld et al., 2016), so these are treated as an additional trait (*Laminated visual centers)* to differentiate between the two.

#### Laminated visual centers with sensory maps of visual space and parallel feature extraction

*Laminated visual centers* refer to the highly ordered and structured brain regions that receive inputs from high-resolution eyes. These include the nested neuropils (or lamina) within the optic lobes of euarthropods and cephalopod mollusks, and the layered retina of complex eyes in vertebrates and some polychaete annelids. The most distinct and easily recognized feature of these regions is their layered organization, which underlies the parallel processing of information (Waessle, 2004; Sanes and Zipursky, 2010). For example, the vertebrate retina has an outer layer of photoreceptors, several middle layers where lateral and serial connections are made, and finally, an inner-most layer, which consists of retinal ganglion cells (efferent neurons) that send their axons to both mid and high-level brain regions (see *Motor hierarchies*). Unlike the vertebrate retina, the octopus retina consists of only a single layer of photoreceptors, but outer cortical layers of the optic lobe, which receives direct input from the retinal photoreceptors, are very similar to the inner layers of the vertebrate retina (Young, 1971; Songco-Casey et al., 2022). Finally, the optic lobe of euarthropods consists of a minimum of two and as many as four laminated neuropils that process inputs from the photoreceptors (Mayer, 2006). Amazingly, some polychaete annelids (Alciopidae), which have complex single-lens eyes that rival those in vertebrates and cephalopods, also have a multi-layered retina like that in vertebrates (Hermans and Eakins, 1974).

Ininsects and vertebrates, which have strikingly similar visual centers and pathways, the different layers within each neuropil underly the segregation of specific lateral connectivity patterns, (Sanes and Zipursky, 2010; Loesel et al, 2013) (Fig. 6). Lateral inhibition, first described in the horseshoe crab (euarthropod) (Hartline et al, 1956; Hartline, 1969), is a classic example of a lateral connectivity pattern, which has several putative functions, including the enhancement of local contrast between light and dark areas and more generally, what is known as ‘predictive coding’ (Srinivasan et al, 1982; Hosoya et al, 2005; Johnston et al., 2019), in which the more predictable features of a stimulus (in both space and time) are inhibited and the more novel and salient features are enhanced. The lateral interactions between adjacent neurons in different layers eventually give rise to different classes of efferent neurons thatencode salient features of the visual surround, such as local contrast, object orientation, polarized light angle and the direction of local and global motion (Nassi and Callaway, 2009, Roska and Werblin, 2001, Gollisch and Meister, 2010).

At the heart of lateral interactions, is the point-by-point preservation of the spatial continuity between photoreceptors at the periphery. This spatial order or *topographic* relationship of neighboring receptors on the sensory surface is preserved in the brain as a *retinotopic* map, which, by virtue of the way light is focused on the retina, forms a nearly continuous spatial map of external visual space. Retinotopic projections to different lamina within the retina/optic lobe and to different brain areas appear to be a common organizational feature in all three CC lineages (Strausfeld 2005; Saidel 1981; Pungor et al 2023). As far as we can tell, retinotopic maps and parallel extraction of features by different cell layers is not characteristic of 1st order visual areas in CC and non-CC phyla receiving inputs from non-imaging median (e.g., ocelli) or other low-resolution eyes.

#### Learning and memory structures

The ability to learn and remember are fundamental skills in the basic cognitive tool kit of all animals (Lyon, 2021; Ginsburg and Jablonski, 2021). Although learning and memory are understandably lumped together, they each involve multiple types, functions and underlying processes (Gallistel and Matzel, 2013; Coolidge, 2019; Ginsburg and Jablonka, 2021). It thus comes as no surprise that learning and memory are not a unitary function of a single brain region or structure in either vertebrates (Poldrack and Packard, 2003; Broglio et al., 2005)) or invertebrates (Messenger, 1983; Hammer and Menzel, 1998). In vertebrates, learning and memory is associated with several interacting brain regions, including the cerebral cortex/dorsal pallium, the cerebellum (Montgomery and Bodznick, 2016; Hull, 2020; De Zeeuw and Brinke, 2022), the hippocampus (Broglio et al., 2015) and the amygdala (Broglio et al., 2005). The same can be said for cephalopod mollusks, for which the optic lobe and frontal and vertical lobe complexes have been associated with visual, chemosensory and tactile-based learning and memory (Young, 1971, 1991; Messenger, 1983; Hochner 2010).

Euarthropod olfactory and optic lobes have also been implicated in olfactory- and visually based learning tasks (Hammer and Menzel, 1998; Tomsic et al., 2003; Sztarker et al 2005; ). Mushroom bodies are the structures most frequently associated with learning and memory in euarthropods (Zars, 2000; Heisenberg 2003; Farris and Dyke, 2015), but the central body complex of insects is also implicated, especially as it relates to spatial behaviors such as navigation (Homberg 2008; Plath and Barron, 2015; Turner-Evans and Jayarman, 2016). At least one of these identified structures for learning and memory, our criterion for this trait, could be documented in five non-CC protostome phyla: Nemertea, Platyhelminthes, Annelida, Tardigrada, and Onychophora.

#### Multisensory integration areas

The convergence of 1st and/or higher-order inputs from more than one sensory modality into a distinct brain region is a common organizational feature of brains in all three CC lineages (see Table 2 in main paper). The behavioral uses and advantages of multisensory integration are many and well-documented for both vertebrates (Ma and Pouget 2008; Stein et al, 2020; Rolland et al, 2022;) and invertebrates (Gronenberg and Lopez-Riquelme, 2004; Dustemayers and Frye, 2010; Leonard and Masek, 2014). For higher-order learning/memory and motor-control regions, multisensory integration appears to be more the rule than the exception. In vertebrates, multisensory convergence sites include the midbrain optic tectum (Stein et al, 2020) and various pallial subdivisions of the telencephalon (Wallace et al, 1992; Stein et al., 2020). Among invertebrates, they include the mushroom bodies (Gronenberg and Lopez-Riquelme 2004; Farris, 2005) and central body complex (Kathman and Fox, 2019) of euarthropods, and the median superior frontal lobe and other higher order motor centers (e.g., basal and peduncle lobes) of cephalopod mollusks (Young, 1971; Messenger 1983). Mushroom bodies are also found in several non-CC phyla (Annelida, Nemertea, Tardigrada and Onychophora), where, as in euarthropods, they are believed to function in multisensory associations for learning and memory (Zars, 2000). At least one of the above identified multisensory integration areas, our criterion for this trait, could be documented in four non-CC phyla: Nemertea, Platyhelminthes, Annelida, and Onychophora.

#### Motor hierarchies

Despite incredible diversity in locomotor modes and mechanisms (Table 1), locomotor control in animals with complex brains is based on a few fundamental principles that rely on multiple processing levels within a hierarchical structure (Orlovsky et al., 1999; Merel et al., 2019). Hierarchical structures consist of higher-order (‘superordinate’) brain regions that generally subsume or ‘control, modify or modulate’ the process in lower (‘subordinate’) regions (Welford, 1951; Miller et al. 1960) (Fig.1). Motor systems in all three CC lineages involve higher-order brain centers in more anterior or superior regions of the brain, and mid to lower-level regions in more posterior/inferior regions of the CNS, including thoracic and spinal cord ganglia (Appendix A, Messenger, 1983; Strausfeld and Hirth, 2013; Cheong et al., 2020).



Figure 1. Hierarchical structure of motor systems illustrating different levels and types (open vs closed loop) of control.  Under open-loop control, behaviors are guided solely by sensory inputs from external sources. Under closed-loop control, animals are continuously guided by the sensory consequences of their own movement through the environment, which feed back onto motor control centers. Adapted from Orlovsky et al. (1999) and Merel et al. (2019). See Appendix Bfor more information about brain structures in the motor hierarchies of different CC lineages.

High-level regions largely play an executive and supervisory role by attending to sensory and internal state (e.g., affect, thirst, hunger) inputs. That is, they make the decision to act and select the appropriate action. High or mid-level regions also supervise the action, by directing the speed and direction of movement by continuously monitoring external sensory inputs to enable animals to e.g., climb over or avoid an obstacle. In contrast, low level regions, which are semi-autonomous, play more of a regulatory role, using sensory reafference (sensory stimulation caused by self-movement), vestibular (body rotational sense) and proprioceptive feedback from joints, muscles and tendons to fine-tune and/or stabilize behaviors, so that animals can e.g., remain upright in the face of environmental perturbations or make compensatory eye movements to prevent blurring when moving the head or body)(see also body motion senses and adaptive filter circuits under sensory and brain traits). Low-level, nearly autonomous regions are particularly well-developed in the suboesophageal brain mass and peripheral nervous system of the octopus for controlling arm movements (Hochner, 2012), but these are nevertheless subject to control influences from higher centers (Mather, 2019).

High-order brain regions in vertebrates include the prosencephalic cortex/pallium and basal ganglia, and mid-level regions include the mesencephalic optic tectum (Appendix A). In cephalopod mollusks, the basal lobe complex in the supraoesophageal mass is a higher order region, whereas the medullary region of the optic lobe and/or the peduncle lobe are putative mid-level regions (Saidel, 1982; Messenger, 1983; Shinego 2018). In euarthropods, high-order regions are the protocerebral mushroom bodies and central body complex (Turner-Evans and Jayerman 2016), the latter of which is thought to be functionally equivalent to the vertebrate basal ganglia (Strausfeld and Hirth, 2013), as are the anterior basal lobes in cephalopod mollusks (Chichery and Chichery, 1987; Gleadall 1990). The inner most neuropil of the optic lobe (lobula plate) of euarthropods also functions as a mid-level control region (Borst et al., 2010; Evans et al., 2019). Interestingly, the lobula plate and mushroom bodies of euarthropods have similar, if not identical positions as the vertebrate optic tectum and visual cortex, respectively, in the dual visual pathways from retina to mid- and high- level brain regions (Sanes and Zipursky, 2010). Our criterion for assigning motor hierarchies to non-CC phyla is that they possess one or more of the mid- to high-level motor centers identified above.

#### Adaptive filter circuits and parallel fiber systems

The mushroom bodies of euarthropods (Farris, 2011) and some annelids (Beckers et al., 2022), the peduncle lobe of the octopus (Messenger, 1983; Shigeno et al., 2018) and the cerebellum and cerebellar-like structures in the vertebrate rhombencephalon (Montgomery and Bodznick, 2016) all share striking cytoarchitectural features. These include (1) a large population of densely packed, small-bodied cells (e.g., cerebellar granule cells and mushroom body Kenyon cells) with long, thin axons that form (2) a massive molecular layer of parallel fiber inputs to (3) an underlying layer of larger efferent (output) cells (cerebellar Purkinje cells and mushroom body lobe efferents) with extensive dendritic arborizations into the overlying molecular layer (Fig. 2).



Fig. 2. Neural architecture of an adaptive filter circuit that can discriminate between self- (sensory reafference) and other-generated components (sensory exafference) of incoming sensory information (see text for further explanation). Redrawn from Montgomery and Bodznick, 2014.

 In vertebrates, these highly ordered structures function as *adaptive filters*, which, amongst other things, ‘learn’ to predict the sensory inputs expected from the animal’s own self-generated movements. This ‘knowledge’ is then used to nullify the ‘self’ component of incoming sensory information (reviewed in Dean et al, 2010; Montgomery and Bodznick, 2016). Adaptive filter circuits do this by comparing (1) motor predictive inputs about self-movement (vestibular, proprioceptive, and motor command information) from the parallel fiber system to the apical dendrites of efferent neurons with (2) sensory inputs from external senses to the cell body or ventral dendrites of the efferent neurons. Efferent neurons thus combine internal predictive information about body motion with external sensory information that includes not only post-facto information on the animal’s own movements (e.g., via optic flow, a form of sensory reafference) but also other information about what’s happening in the external world. As Montgomery and Bodznick (2016) put it, the adaptive filter picks ‘the best combination of thousands of prospective predictive signals’ from parallel fibers to construct a negative, cancellation waveform of the self-generated contribution to any incoming sensory information from ventral inputs.

The shared cytoarchitectural and connective features of cerebellar, mushroom body and peduncle lobe brain regions in CC lineages raise the tantalizing specter that they all function as adaptive filters. Indeed, the peduncle lobe of cephalopod mollusks is employed in vestibulo-ocular reflexes (Budelmann and Young, 1984) not unlike those involving adaptive filters in vertebrates, in which the eyes move reflexively in response to a moving head (or visual field) in order to cancel the blurred image that would have otherwise occurred had the eyes been fixed in the head (Montgomery and Bodznick, 2016). Adaptive filters also play a role in discriminating motions due to self from those due to ‘other’, and in predicting the consequences of one’s own actions and thus, in principle, forming a nascent sense of agency (Montgomery and Bodznick, 2016; Hull, 2020). In a more general sense, adaptive filters in cerebellar-like structures might be regarded as a ‘plastic, internal representation of the sensorimotor system… that is used to predict, rehearse and thus, optimize an animal’s own motor performance’ (Stein and Glickstein, 1992). Although a few non-CC phyla (Platyhelminthes, Onychophora, Annelida) have mushroom bodies, the extent to which they function as adaptive filters is presently unknown, as it is in all protostomes (Farris, 2011). Nevertheless, mushroom bodies have the necessary circuit elements and their presence in animals that actively search for food and mates is entirely consistent with the proposed importance of adaptive filters in active sensing (Farris, 2011). Here, we take a liberal, albeit somewhat speculative approach and include all protostome phyla with mushroom bodies, as well as other phyla with similar parallel-fiber architectures as possessing adaptive filters.

## 5. Cognitive and behavioral traits

Cognitive traits are generally difficult to assess, as they depend on behaviors to reveal them – either in the form of natural behaviors that are observed in the wild or in terms of natural or trained behaviors used in experimental settings to measure cognitive abilities. Here we describe three forms of experimentally determined learning abilities as cognitive traits that range from simple to complex. Behavioral traits consist of two naturally occurring behaviors - central place foraging and construction behaviors that highlight place (or navigational) and object-oriented skills, respectively. Relative to more basic behaviors (like locomotion – see motor traits), these two natural behaviors are cognitively complex in that they involve a number of different skills and cognitive abilities.

#### Non-associative (NA) learning

NA learning, which involves a change in responsiveness to a repeated stimulus, has two forms, which are nearly mirror images of each other: habituation and sensitization. In habituation, the strength, or probability of a response to a given stimulus decreases after repetition; the animal has learned to disregard the stimulus. In sensitization, the response strength or probability increases; the animal has learned to respond to this stimulus. These forms of learning, which do not require neurons or a brain, are very ancient and widespread, and are exhibited by all multicellular and even single-celled organisms, such as paramecium (Ginsburg and Jablonka, 2021). We were able to find published evidence of these forms of learning in 11 of the 17 lineages (Perry et al., 2013, Prados et al., 2020; Cheng, 2021).

#### Limited associative learning (LA)

Associative learning (so-called Pavlovian conditioning) describes the ability of animals to make connections between sensory stimuli, contexts and actions, in a variety of ways (Moore 2004). A simple (limited) (Ginsburg and Jablonka, 2019) form of associative learning is classical conditioning, which enables individuals to associate one stimulus with another, so that e.g., a cat salivates (unconditioned response) in anticipation of food (unconditioned stimulus) with the sight or scent of a food can being opened (conditioned stimulus), or a minnow can associate the scent of a predator with alarm pheromones produced by conspecifics. One way that classical conditioning is more limited than more complex forms of associative learning is that it generally applies to relatively simple, reflexive or unconditioned behaviors, such as eye blink reflexes to puffs of air or a dog salivating to the smell of a piece of meat. LA learning can also involve operant conditioning (when animals make associations between voluntary actions and their consequences) (Moore, 2004), but only when stimuli and actions are relatively simple – e.g., turning right in a T maze when a light comes on to avoid shock. LA learning has been documented in fewer phyla (only 9) than NA learning (Thompson and James, 1955; McConnell, 1966; Perry et al. 2013; Cheng, 2021; Ginsburg and Jablonka, 2019; Loy et al., 2021; Botton-Amiot et al., 2023; Nador et al, 2023), consistent with its intermediate status along the simple to complex continuum.

Unlimited associative learning (UAL)
UAL is defined by Ginsburg and Jablonka (2016; 2021) as a suite of component learning abilities that together enable adaptively flexible object-oriented and goal-directed behaviors, thus being the most complex of the three forms of learning described here. According to the same authors, UAL is found only in vertebrates, cephalopod mollusks and euarthropods (reviewed in Perry et al, 2103; Ginsburg and Jablonka, 2019 and Loy et al, 2021), and thus is the least widespread category of learning. UAL involves operant conditioning, a form of learning in which animals learn by trial and error in successive ‘baby’ steps to perform a wide range of behaviors, even those that are not (at least initially) part of the animal’s natural repertoire (e.g., pressing a lever). Compared to simpler forms of learning like classical conditioning, operant conditioning involves more reliance on learned valences (e.g., animals learning that pressing a lever has positive value because it leads to food) and memories of affective states (e.g., animals remembering ‘feeling good’ after pressing the lever the last time because it led to a positive outcome). Perhaps even more importantly, UAL entails associations between compound stimuli (objects) that represent configurations of lower-order stimuli (edges, shapes etc.) that have themselves been learned through associative learning. For example, animals might need to learn that the associations (relations) between objects, rewards, and actions can themselves change or be sensitive to context, e.g., that an experimenter might reinforce an object in different locations or under different stimulus conditions.

#### Construction behaviors and object-oriented cognition

Although tool use and manufacture are often the ‘go-to’ behavioral indicators of complex cognition, examples are relatively rare compared to widespread construction behaviors that are arguably as good, if not better indicators of complex cognitive abilities (Hansell and Ruxton, 2008; Guillette and Healy, 2016; Perry and Chitka, 2019). Construction behaviors involve the manipulation of raw materials to construct all sorts of housing and other structures. As such, they epitomize one of the key characteristics of complex (aggregate) systems in that they actually shape the animal’s external environment (Manson, 2001). Structures include (1) elaborate tubes built from pieces of shells, algae and detritus by polychaete tube worms (Pardo and Amaral, 2006), (2) the complicated and often towering mate-attracting bowers and (3) garden-variety nests built by birds from all sorts of found materials (Madden, 2000; Guillette and Healy, 2015; Breen et al. 2016), (4) the architecturally impressive and multifunctional dams, nests and hives built by beavers and insects (Karsai and Wenzel, 2000; Sabino et al., 2017; Gallo and Chittka, 2018; Park et al, 2022), (5) the intricately woven silk webs produced by orb-weaving and other spider species (Boultry and Blamires, 2013; Hesselberg, 2015; Eberhard 2019;) and (6) the dens excavated from discarded shells by octopi (Scheel et al., 2018). Female octopi are also use their arm suckers as bobbins to weave egg stems together to form a kind of hanging ‘incubator’ in their shelter (Mather, 2019).

Construction behaviors require object-oriented cognitive skills. These include the ability to process multisensory pieces of information, such as colors and visual patterns, scents, flavors, tactile, proprioceptive and kinesthetic sensations, so that they can be combined and attributed to a single source (the object to be manipulated). They may also involve the ability of animals to identify, categorize or otherwise evaluate objects in terms of their suitability for the intended purpose. Finally, they entail the complex spatiotemporal movements of the body and body parts to grasp an object and control its orientation and/or location in space. The act of reaching/grasping alone involves a complex hierarchy of control decisions and dynamic interactions between the body and the object in a goal-directed fashion (Trestman 2013; Sugasawa et al, 2021).

Despite the complexities described above, construction behaviors, particularly those by euarthropods, have often been viewed as being highly stereotyped, relying on genetically pre-programmed routines that do not require complex cognitive abilities. However, more recent assessments of construction behaviors reveals that they are highly flexible (Hesselberg, 2015; Gallo and Chittka, 2018; Eberhard, 2019; Perry and Chittka, 2019), one of the hallmarks of complex systems (Manson, 2001) and cognition (Emery and Clayton, 2004). That is, construction behaviors can be modified to meet different goals or performed in substantially new ways to overcome novel challenges. Honeybees, for example, are able to build hives with novel, variant geometries when their favored shape of cavity is not available, indicating that advance planning is used to meet each space requirement (Gallo and Chittka 2018; Perry and Chittka, 2019). Paper and mud nests built by wasps likewise exhibit a huge range of variability, according to available raw materials and structural requirements, especially as they relate to the strength and thermoregulatory properties of the structure (Jones and Oldroyd, 2006; Hocherl et al., 2016). As another example, the making of elaborate bowers for attracting mates appears to involve observational learning and practice by juvenile male bowerbirds (Vellenga, 1986; Maxwell, 1999) and perhaps even innovation, as adult males compete to make their bowers more attractive to females (Frith et al, 1994; Madden, 2001).

As documented above, examples of construction behaviors appear to be restricted to the three CC lineages (vertebrates, cephalopod mollusks, and euarthropods) plus one non-CC phylum (Annelida).

#### Central place foraging and place-oriented cognition

Bell (1992) defines central place foraging (CPF) as a pattern of space use in which animals go on routine foraging trips to find resources and bring them back to a central place, often shared with others (e.g, a beehive or birds' nest). CPF entails a wide range of sensory cues and navigational strategies that vary in terms of cognitive complexity. Moreover, CPF is a multidimensional behavior (Sommer et al., 2017).

Simple strategies include the use of chemical scent trails, which, in many cases are directionally polarized, so individuals can use a network of previously laid trails to recover their home position over a wide territory, even when individual territories overlap (Chelazzi, 1990). At the more complex end of the cognitive continuum are *geocentric* strategies (sensu Grob et al, 2021), which rely on spatial memory and allocentric cues about the spatial relationships of different landmarks to each other, to form so-called ‘cognitive maps’ of space (Tolman, 1948; Jacobs, 2003; Liu et al., 2019). Perhaps somewhat intermediate in complexity, are *egocentric* strategies based on information about the relationship of the animal to its home position and travel path at different times on its outbound journey (so-called path integration). Regardless of the sensory cues and navigational strategy, CPF presents a substantial cognitive challenge that requires place-oriented cognitive skills. That is, animals must be able to identify and establish a suitable home location (in some cases, constructing them), find locations where resources are available, pick them up for transport, regulate the load according to how far they have to go, then find their way home from different directions and locations each time they venture out on a foraging trip, all while negotiating obstacles that might be in their way. Outbound foraging trips can also be very far away from the central cite. Foraging bees, for example, fly up to 8 km away, whereas land-based ants go as far as 9 m.

CPF has been reported in numerous vertebrates, including mammals, birds and teleost fish and sharks (Olsson and Bolin, 2014; Papastamatiou et al., 2018). Within euarthropods, the narrow-waisted hymenoptera (Apocrita) offer a wealth of well-documented examples. Tens of thousands of species of bees, wasps, and ants provision nests through repeated forays for building materials, nectar, pollen, water, and/or prey (Holldobler and Wilson, 1990; Gathmann, 2002; Evans and West-Eberhard, 1973 ). Octopi are also central place foragers, leaving their den to forage, often bringing the food back to the den for consumption (Mather,1991, 2006; Grasso and Basil, 2009).

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