# Appendix C: Cognitive groundwork laid by brain traits

In the main body of the paper, we describe how a pivotal brain trait – 1st-order laminated visual regions of the brain might lay the groundwork for complex cognition. Here we provide several more examples of how intermediate brain traits could have built the foundation for (1) learning and prediction, (2) behavioral flexibility and (3) spatial navigation and associative learning.

## 1. Adaptive filter architectures as neural scaffolds/motifs for learning and prediction

The neural architecture associated with known adaptive filter function resides in the cerebellum and hindbrain sensory regions of vertebrates (Montgomery and Bodznick, 2016; Fig. 1). This distinct architecture is characterized by (1) a large population of densely packed, small-bodied cells (cerebellar granule 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) with extensive dendritic arborizations into the overlying molecular layer (Fig. 1). Small interstitial cells with long, thin axons similar to cerebellar granule cells can be found in brain structures associated with learning and memory in other CC lineages – e.g., in the mushroom bodies of euarthropods, where they are called Kenyon cells (Farris, 2011), and in the peduncle lobe and vertical lobe complex of the octopus brain (Hochner, 2010). In the octopus brain, over 25 million amacrine cells are packed into the vertical lobe complex, which contains more than half the number of cells, but only a small fraction of the volume of the supraoesophageal mass (Maddock and Young, 1987). Similarly, it is estimated that cerebellar granule cells make up close to 70% of the total number of cells in the human brain (Azevedo et al., 2009; von Bartheld et al 2016, Montgomery and Perks, 2019) even though the cerebellum itself is less than 10% by volume (Montgomery and Bodznick, 2016). Like cerebellar granule cells, mushroom body Kenyon cells and vertical lobe amacrine cells make multiple synapses with the apical dendrites of large efferent neurons (Fig. 1).



Fig. 1 Neural architecture of an adaptive filter circuit that can discriminate between self- (reafference) and other-generated components (exafference) of incoming sensory information (see text for further explanation). Redrawn from Montgomery and Bodznick, 2016.

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. As such, they 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). This ‘self-knowledge’ is 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 (Fig. 1). 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. As such, this neural motif may be a hallmark of certain types of learning processes wherever they are found. Thus, the vast amacrine-Kenyon-granule cell inputs to a much smaller population of efferent neurons in vertical lobe/mushroom body/cerebellar-like brain structures in CC animals may all represent functionally equivalent neural motifs for adaptive filter function, even though the learning and prediction outcomes may vary. Moreover, recent evidence indicates that circuits like these in the vertebrate cerebellum also support rewards-based learning used in higher cognitive processes (Hull, 2020).

As a final note, adaptive filter circuits in cerebellar-like structures and lateral-inhibitory circuits in laminated visual regions of the brain both have a predictive function associated with them. Whereas adaptive filter motifs predict the sensory consequences of self-produced motion for the purpose of canceling it out, predictive coding motifs in the vertebrate retina and perhaps also, the optic lobes of euarthropods and cephalopod mollusks suppresses expected/predicted visual ‘noise’ for the purpose of boosting the salience of novel and unexpected features (Srinivasan, 1982; Hosoya et al., 2005; Johnston et al., 2019).

## 2. The visuomotor hierarchy as a global scaffold for behavioral flexibility

As an organizational construct, the motor hierarchy is at the heart of behavioral flexibility, one of the hallmarks of complex cognition (Emery and Clayton, 2004). Indeed, hierarchies of all sorts are considered to be general reflections of complexity (McShea, 2001; 2021). Motor hierarchies rely on information about both the internal and external world of the animal to make decisions about when to act and what action to take (see Appendix B: Brain traits).

 Visuomotor pathways, in particular, appear to play a dominant role as a global scaffold for this purpose. In fact, Butler (2000) proposed that the descending visuomotor pathway (= motor hierarchy) in early vertebrates served as a template for the patterning of ascending pathways of other sensory systems (e.g., auditory, lateral line, electroreception), thus playing a prominent role as a scaffold for multisensory integration. Memory and learning systems also appear to be distributed along the visuomotor hierarchy (see Appendix A: Brain Traits), especially as they relate to motor learning and the potential use of stored memories for planning future actions. Distributed rewards systems, which are important for valuation (learning whether something is potentially beneficial or harmful) go hand in hand with learning and memory, adding another layer to the decision-making levels of motor hierarchies (Wise, 2004; Huber et al., 2011; Perry and Barron, 2013; Porcelli and Delgado, 2017). Finally, diverging visuomotor pathways and subsystems (described below), corresponding to different kinds of behavioral actions, add behavioral flexibility to motor hierarchy scaffolds. The subdivision of visuomotor systems according to behavior is important evidence for the premise that vision evolved for the control of biologically relevant behaviors, rather than for perception of the visual surround per se (Milner and Goodale, 2006).

Visuomotor hierarchies in all three CC lineages can be subdivided according to two distinct locomotor modes of behavior, each controlled by different sensorimotor circuits and pathways – a very ballistic (rapidly accelerating) mode for transient escape maneuvers and a slow to moderately fast mode of locomotion for sustained travel (Berg et al 2018). The sensorimotor circuits underlying ballistic escape maneuvers, such as the well-known giant neuron systems in fish, crayfish, cockroaches and cephalopod mollusks (Camhi, 1980; Edwards et al, 1999; Eaton et al., 2001; Berg et al., 2018; Otis and Gilly, 1990; Shigeno 2018) are designed for fast defense and flight reactions. The giant neurons in these systems can be viewed as bypassing higher motor centers for the sake of expediency, having their own on-board multisensory integration centers for rapid on/off command decisions and crude directional control. In some cases, these fast networks are also coopted for other types of ballistic behaviors – e.g., the partial use of Mauthner cell circuits for the ballistic strike behaviors of some predatory fish (Liu and Hale, 2017).

The sensorimotor circuits underlying slow to moderately fast locomotor actions can be further subdivided into two major and distinct visuomotor pathways, one that culminates in mid-level motor centers (the optic tectum in vertebrates and the lobula plate in euarthropods) and one that culminates in high-level motor (or premotor) centers (cerebral structures in vertebrates, protocerebral structures in euarthropods) (Sanes and Zipursky, 2010)(Fig. 1). Visuomotor pathways in cephalopod mollusks are less-well documented, but efferents from the optic lobe terminate in the lateral basal lobe, a high-level motor control region (Saidel, 1981), and a distinct, internal region of the optic lobe, known as the medulla, may play a mid-level motor control and associative function, as it receives inputs from other regions of the brain besides the outer cortical layers of the optic lobe (Saidel, 1981). The peduncle lobe, which is medial to the medulla, is also a putative mid-level visuomotor control center (Messenger, 1967).



Figure 1 (same as Fig. 4 in main paper) Laminated visual centers that preserve the spatial order of photoreceptive inputs as retinotopic maps and that use parallel processing in different layers to extract different spatiotemporal features of high-resolution visual inputs. Projections from efferent neurons follow two major pathways that culminate in mid- (yellow) and high-level (blue) motor regions in vertebrate, euarthropod and cephalopod mollusk brains. Layers include the photoreceptive layer (red), intermediate processing layers of interneurons with lateral interconnections (blue) and efferent layers (green). Efferent cell layers provide the main outputs to other regions of the brain. Inspired by the text and figures in Sanes & Zipursky (2010).

Mid-level visuomotor centers in vertebrates and euarthropods underly simple orienting behaviors to local targets (e.g., prey) or the nearby surrounding environment via optic flow, utilizing an egocentric (where things are relative to self) framework. Orienting behaviors include the closed-loop optomotor responses of swimming fish (Northmore, 2011) and flying insects (Borst et al., 2010; Srinivasan, 1992) to optic flow, created by an animal’s movement relative to a stationary surrounding. They also include more open-loop orienting responses, including the rapid repositioning of the eye, head, or whole-body to novel stimuli, such as those mediated by the optic tectum in vertebrates (Stein and Meridith, 1993; Gandi and Katnani, 2011) or the lobula plate in euarthropods (Land, 1969; Marshall et al., 2014; Jacob et al., 2018; Bruce et al., 2021). The rapid movements realign an animal’s sense organs so that they are facing the stimulus source and thus, place the animal in a better position to approach, grasp, or further explore it with vision and other senses.

In contrast, the final evaluation of and decision to respond to a novel stimulus, as well as long-range navigational abilities using allocentric (where something is relative to something else) or geocentric (where something is relative to the surrounding earth) cues likely involve the second visual pathway terminating in the visual and premotor centers of the vertebrate cortex (Milner and Goodale, 2006) and in the protocerebrum (mushroom bodies and/or central body complex) of euarthropods. Mushroom bodies, in particular, have been implicated in spatial learning and navigation in euarthropods (Mizunami et al., 1998; Buehlmann et al., 2020), as has the hippocampus in vertebrates (Broglio et al., 2003; 2015). As such, these high-level structures function more in proactive behaviors, such as the planning by central place foragers of an outbound trip to find a needed resource.

Furthermore, the computational principles underlying representations of ego- and allocentrically mapped space are fundamentally different. The optic tectum and lobula plate, for example, rely on retinotopic maps (Medan et al., 2015; Gandhi and Katnani, 2011). Thus, direction in space can be mapped relative to a body-centered (egocentric) frame of reference, the head or eyes. A central principal of operation in the vertebrate optic tectum is that non-visual maps of space (e.g., auditory maps of sound direction based on binaural time and intensity cues) in layers just below the surface of the optic tectum are in spatial register with retinotopic maps of visual space in superficial layers. Thus, the optic tectum is a prominent site of multisensory convergence that seamlessly integrates information from different senses into a spatially unified image. Deeper layers are thought to dynamically map motor-error in egocentric coordinates, providing the necessary instructions for animals to move in a direction that corrects or diminishes the motor error, defined as the angular gap between the animal’s heading and the stimulus source)(Sparks, 1988).

 On the other hand, more proactive, long-range navigational abilities mediated by the second visuomotor pathway rely more on a spatiotemporal representation of where an animal is with respect to different locations in the environment built up over time and involving more complex cognitive abilities, such as cognitive maps or path integration. At the risk of oversimplifying, the cognitive tasks associated with the second pathway might be described, at least in part, as being ‘place-oriented’ (or ‘relationship-oriented’, Eichenbaum, 2017), whereas those for the first pathway as more ‘object -oriented’ (Dicke and Roth, 2009; Wullliman and Vernier 2009; Bianco and Engert 2015; Medan et al., 2015).

## 3. An olfactory-driven cognitive groundwork for spatial navigation and associative learning

The unique or nearly unique distribution of visually related traits in CC lineages have led us to emphasize groundwork scaffolds and neural motifs related to visuomotor processing. However, Jacobs (2012, 2023) makes a compelling case for the importance of olfaction in developing the groundwork for cognitive maps and learning and memory in the context of spatial navigation. Given that the earliest life forms evolved in nearly total darkness in and under thick biomats, (Sielacher, 1999; Plotnick et al., 2010), and odor plumes carry information over long distances, olfaction would have been a prominent and likely first source of information about the physical nature of the early marine environment (Ache and Young, 2005; Jacobs 2012; 2023; Kamio and Derby, 2017). Moreover, as Dusenbery (1992) points out, chemical stimuli like odors do not require additional transduction steps or structures, such as lenses or dense stones (otoliths) (which take time to evolve), to convert the stimulus energy into meaningful sensory signals. Rather, the odor transduction process involves direct biochemical reactions at the cell surface. Thus, the ability to sense distant odors would likely have been present in the very beginning of multicellular life.

 Simple navigational strategies are available to animals that use odor gradients, such as klinokinesis by nematodes (Rengarajan and Hallem, 2017), or odor trail-following by terrestrial gastropod mollusks (Ng et al., 2013). However, the information provided by odors about the whereabouts of a distant odor source, especially in the aquatic environments where life began, is not nearly as fast or as reliable as that typically provided by light (see Appendix C). For one thing, odors diffuse into the surrounding water, dispersed by water currents in an irregular fashion in all but the most stagnant of waters. As a result, efficient odor tracking strategies rely on other sensory cues, such as flow-sensing to orient upstream in order to find odor sources (Gardiner and Atema, 2007; Baker et al., 2002; Carde and Willis 2008). Moreover, multimodal integration of different spatial cues is apparently critical to the calibration of cognitive maps used in spatial navigation (Jacobs, 2012). Thus, olfactory-guided spatial navigation requires multisensory information, as well as an ability to learn and interpret complex spatiotemporal patterns of odor inputs (Osorio et al., 2014). As a result, the evolution of higher-order brain targets of olfactory inputs (e.g., hippocampus in vertebrates and mushroom bodies in euarthropods (Broglio et al., 2015; Strausfeld et al., 1998) could have provided a basic scaffold for spatial odor mapping, combined with multisensory integration and learning and memory circuits. Indeed, Jacobs (2012) argues that the mapping of odorants for spatial navigation may have been “the first and primary driving force in the evolution of associative learning”. In any event, olfaction per se, given its wide distribution, is far from being unique to CC lineages (see multi-trait pyramid in main body of paper), and the same can be said for limited forms of associative learning, which is shared by at least 9 lineages. Thus, olfaction by itself cannot explain the emergence of complex cognition in only three CC lineages. However, first-order processing areas for olfactory inputs (olfactory lobes or bulbs), shared by all three CC lineages, are shared with only two other non-CC phyla (Annelida and Onychophora)(Fig. 1). Interestingly, the internal organization of olfactory lobes into distinct glomeruli, which presumably underly chemotopic maps of different types of odors (Luo and Flannagan, 2007), is apparently missing in mollusks (Cummins and Wyeth, 2014; Scaros et al., 2018) and thus, non-essential to the emergence of complex cognition. In euarthropods, as well as in some annelids and onychophorans, higher-order motor centers, such as mushroom bodies, receive olfactory inputs from the olfactory lobes (Strausfeld et al., 1998), as well as other sensory inputs to play a prominent role in learning and memory. Thus, a role of olfaction, combined with other senses, in associative learning and geocentric strategies for spatial navigation cannot be discounted and is even, in our opinion, likely.

As a final note, there has been a major evolutionary shift from an olfactory- to visually- dominated telencephalon in land vertebrates relative to primitive aquatic vertebrates (Streidter and Northcutt, 2020; MacIver and Findlay 2022). This shift is largely due to a million-fold increase in the volume of visual space during the land-to-water transition of vertebrates (MacIver and Findlay, 2022) (see also Appendix C). Thus, telencephalic circuits originally devoted to olfactory processing, perhaps in connection with olfactory-based navigation, could have later been coopted for higher-order visual processing associated with place-oriented, as well as other forms of more complex cognition.

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