is initiated due to an imbalance of neuron activity between hemispheres (Ivano et al., 2010; Zorović and Hedwig, 2013). With this set-up, the actuation difference between left and right achieved should be high, so that the force generation difference is big enough to steer. Therefore, the connection from the inhibitory neurons to the output neurons (w_{IO}) should be strong.

In the Comprehensive network we suggest a split into turning and velocity neurons due to optic flow integration in descending neurons in bees and the latest discoveries in the descending neurons of *Drosophila*. Descending neurons have been shown to innervate different groups of muscles: while some groups target muscle groups which are more involved in power generation, others target muscle groups which are more involved in steering (Namiki et al., 2018). Unilaterally descending neurons in *Drosophila* have been shown to code for velocity (Bidaye et al., 2020). Some of unilaterally descending neurons show bilateral innervation of the motor centers (Bidwell and Goodman, 1993). Functionally, this could control walking velocity across both sides of the motor centers. Other Type II neurons have been shown to be involved mostly in steering (Schnell et al., 2017; Rayshubskiy et al., 2020). Also, Type I neurons are involved in steering (Ivano et al., 2010; Zorović and Hedwig, 2013; Namiki and Kanzaki, 2016). Animals (insects) steer their bodies while walking by pushing the outward actuators away from the body while pulling in the actuators on the inside (Mantziaris et al., 2020). Both actuator centers therefore can produce both left and right turns individually. Fiore et al. (2017) suggested a similar pre-motor command structure (walking forward, left, and right in both LALs), yet more abstract than our Comprehensive model. The biggest difference to our models is the assumption that the LAL neurons are inhibited by CX neurons (Fiore et al., 2015).

However, evidence suggests that the meta-motor commands could be more nuanced than this. In cockroaches, recording of CX neurons show how different units encode for different walking directions and velocity (horizontal representation) (Martin et al., 2015). In flying insects like bees, different descending neurons are activated by different directions and velocities of optic flow, therefore coding for pitch, roll and yaw (vertical representation) (Ibbotson, 1991; Bidwell and Goodman, 1993; Goodman et al., 2002). This could mean that motor commands are encoded in a three-dimensional vector space, where a neuron encodes for a specific movement direction in an idiosyncratic manner, as well as the velocity into that direction. Therefore, motor command encoding could possibly be representing walking movements and flying movements separately, or when in either state, only a subset of all possible motor commands could be active.

Another question is how both the left and right descending commands are coordinated. While for a rotation an imbalance of activity between left and right may be sufficient to initiate rotational movements (steering), how are translational movements coordinated? We know from both walking and flying insects that these movements are used (Ravi et al., 2019). This would point toward an identical motor command representation in both pairs of the LAL, where both hemispheres encode omnidirectional movements and velocities, and the consequent motor group innervations are mirror symmetrical.

5. Conclusion

We have investigated the network dynamics of a spiking neural network model inspired by the Lateral Accessory Lobe of the insect brain. The network dynamics produce a stimulus reliability dependent small scale search behavior. That behavior can be produced over a variety of parameter combinations and noise levels, speaking of a robust network. Furthermore, other generated behaviors resemble naturally occurring behaviors of navigating animals.

In preliminary simulations we investigated the network in a simple navigation setting (Steinbeck et al., 2020b). We found that the generation of small scale search movements, which are directly modulated by the reliability of sensory signals, can improve the success of approaching a target. In future studies we want to incorporate this model with more complex visual stimuli (Risse et al., 2018), and additional modalities like optic flow (for the CPG adaptation mechanism Pansopha et al., 2014) or optomotor response (Bidwell and Goodman, 1993) or olfaction (Ando et al., 2013) and navigation models (Vöel and Wystrach, 2020; Sun et al., 2020).

Data availability statement

The datasets presented in this study can be found in online repositories. The name of the repository and accession number can be found at: GitHub, https://github.com/FabianSteinbeck/SNN-LAL-CPG.

Author contributions

FS developed the hypotheses, designed and programmed the neural networks, and performed the experiments and analysis. He furthermore wrote the manuscript. PG helped with experimental design and analysis, and editing of the manuscript. TN supported the design and development of the neural networks and editing the manuscript. AP supported with editing the manuscript. TN, AP, and PG acquired