The tools that *D. melanogaster* provides can be utilized to answer questions on CS encoding, function, and network dynamics; however, their small limbs impose a restriction on the accurate measurement of limb forces. Interestingly, drosopholids have CS in locations that are homologous to other insects, but it is unclear how the animals’ extremely small size and low weight affect the role and function of CS during walking. Previous work of Dinges et al. (2021) laid out multi-faceted, biological experiments on leg CS in *D. melanogaster*. This work connected outer CS morphology with the substructure morphology of CS fields and their function during strain simulation as well as the neural components of CS that are interconnected with CS morphology, informing on their influence on movement and coordination. For the analysis of both fine and gross morphology of CS, scanning electron microscopy (SEM; Figure 2B-D) was used to investigate interindividual (Figure 2C) and interleg (Figure 2D) morphological variability. The corresponding biomechanics of the fine morphological structures were investigated using a nano-computed tomography-based (nano-CT) model.

Previous models of CS mechanical properties were based on numerical or analytical modeling and did not combine morphological data with authentic cuticular strain data (Cocatre-Zilgien and Delcomyn, 1999; Kaliyamoorthy et al., 2001; Sane and McHenry, 2009; Skordos et al., 2002; Vincent et al., 2007). Although these models are highly informative, they are based on simplified CS morphology and cuticular characteristics (Sane and McHenry, 2009) and had to make assumptions about strain for the sake of simplicity. To advance the knowledge on the interaction of strain with CS, finite element analysis (FEA) was used to investigate the strain distribution in the FeF of *D. melanogaster* (Figure 2B; Dinges et al., 2021). The FeF CS, which vary in key morphological parameters (orientation, eccentricity, collared presence), have partially interconnected sockets. The model showed that the sockets seem to be displaceable entities with their own directional sensitivities and that they influence strain distribution by transforming the stimulus along their axis. By further altering the material parameters of collars, we could identify their influence on the displacement of the entire field. This underlined that two structural components, sockets and collars, function in the amplification and distribution of strain.

To connect the different CS locations along each leg with their function during movement, I indentified driver lines that label CS in the trochanteral field (TrF) and FeF and transiently activated (CsChrimson; Klapoetke et al., 2014) and inactivated (GtACR1; Mohammad et al., 2017) these neurons in intact, behaving flies to test their necessity and sufficiency for leg movements and postural control. The results showed that inactivating small groups of CS in walking flies and activating them in quiescent flies affected inter- and intraleg coordination as well as leg movements. These effects varied between leg types during both inactivation and activation. For example, during inhibition, the front legs commonly showed different effects on kinematic parameters compared to the the middle and hind legs (e.g., increased swing duration vs. decreased swing duration). Whether this is due to differences in strain in each leg or the neuronal processing of strain signals is unclear; this can be tested using robotic systems that are capable of determining differences in strains within each leg (Goldsmith et al., 2020).

Activating CS of the TrF and FeF in quiescent animals (with and without ground contact) significantly altered multiple joint angles, indicating that trochanteral and femoral CS can modulate muscle synergies. Taken together with the knowledge on outer morphology and intra-field biomechanics, these novel results underline the relevance of strain sensors for walking behavior in insects and their complexity as mechanosensors in a highly dynamic system. To complete the picture, however, real strain profiles produced during movement need to be determined; this will allow future investigations to correlate phasic strain profiles with CS compression and the consequent effects on the relevant neuronal network components. As state-of-the-art force plates cannot reliably produce force measurements at the minute scale of *D. melanogaster*,and there are no measurements of ground reaction forces for such light-weight organisms, future experiments should utilize dynamically scaled robotic systems to estimate physiological forces during movement.

The forces experienced by a robot can be compared to those of a fly if the robot and its motions are dynamically scaled to match the fly. However, one must address how the dynamics of a fly differ from those of a larger animal or robot; and how important load sensing is for a small, light insect such as the fly. While walking, an animal experiences some combination of gravitational forces pulling downward, inertial forces due to its mass and acceleration, elastic forces from its muscles and joint membranes, and viscous forces due muscles sliding through the cuticle as they extend and contract. Large and small animals are disproportionately massive; mass scales differently with size than do elasticity and viscosity of muscles (Hooper 2009, Sutton 2021). As a result, a human’s limbs hang down with gravity when their muscles are relaxed, and the nervous system may need to actively control momentum during rapid movements (Popovic et al., 2004). In contrast, the limbs of small animals, such as *Drosophila*, are disproportionally dominated by elastic and viscous forces. The resting posture of even moderately-sized insects such as the locust (Ache and Matheson, 2013) and stick insect (Hooper et al., 2009) exhibit passive joint forces that return the limb to a particular posture, no matter the direction of gravity. Thus, a robotic model of an insect should also be dominated by elastic and viscous forces. Because robots are not constructed from biological materials, and thus do not follow the same relationships between mass, spring stiffness, and length, a robot of any size can be designed to model an insect by adding elastic components to the leg joints to enforce same balance between gravitational, inertial, elastic, and viscous forces experienced by the animal. Such considerations were central to the design of Drosophibot, the research robot to be used for this project, which is further discussed below (Goldsmith et al., 2020).