Supporting Information

S1 PDF – **Additional Experimental Data for Standing and Searching Movements**

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As supporting information, we provide further supporting information and discussion on two further behaviors and how these relate and could be realized in neuroWalknet.

Standing

In the Introduction (sect. 2), we mention six motivation units, representing states Stand-Walk, Forward-Backward, Stance-Swing, but did not address examples concerning state Stand. As, however, Standing embraces an important aspect of behavior, in the following, we will briefly sketch cases concerning state Stand that form a necessary complement to walking behavior.

At first sight, standing seems to be a simple subcase of walking, as in the current version of neuroWalknet, just switching the global velocity value to zero is sufficient. However, the following will illustrate the complexity of this behavior, and will show that the structure of neuroWalknet based on motivation units, here Stand and Walk, may provide a relatively simple way to integrate both aspects, standing and walking. Four behaviors concerning the way how to deal with external forces will be addressed.

Biological Experiments: When the intact animal is standing freely and with all six legs each on a 3D force transducer platform, spontaneous changes of the torque in one joint can be observed in all legs, and other torques may change too, but in such a way that nonetheless the position of neither legs would change. This behavior led to the interpretation that in state Stand all 18 joints are controlled by negative feedback controllers each equipped with a position integrator [1, 2]. As a consequence, the body and the leg positions stay absolutely fixed although the torques of the individual legs may change considerably and apparently seem to approaching a minimum value. The network studied by Schmitz and Stein [3] may provide a way to optimize these force distributions between the legs via minimizing cuticular stress.

However, over very long temporal periods another behavioral property, called “flexibilitas cerea”, studied in detail by [4] shows that leg positions may change, too, but very slowly, possibly to minimize the sum of all torques even further (review [5]). When, however, not only—as in the cases mentioned above—the own body weight has to be supported, but stronger, permanent external forces have to be counteracted, further mechanisms are activated. To study this behavior in more detail, the reactions of individual leg joints to disturbances have been recorded, while the body was fixed to a holder. In this situation, first the joint develops a significant torque to counteract the external disturbance, but over time this force is decreasing. This behavior can be interpreted as a negative feedback controller with phasic-tonic dynamics ([4, 6, 7], Simulations: [8]).

As a further case—as in the interim situation between dealing with small loads (in comparison with the own body weight, [1, 2]) and stronger external forces as above [4]—, experiments have been performed, where the external forces where characterized by variable elasticity. When the external elasticity was low (i. e., stiffness high)—similar to case (2)—the joint controller showed a phasic behavior. However, with lower stiffness, the joint kept its position in place for a long time (for details see [9, 10]).

Some of these behaviors have been simulated individually, but not jet integrated into a global structure as neuroWalknet. These could be integrated into neuroWalknet via unit Stand and may thereby in future work combine walking with standing.

Searching

Searching movements have been studied in stick insects with fixed body and partly restrained legs (e.g. [11–13] in detail, but also in free walking animals [14–16]). In neuroWalknet, searching movements are assumed to be controlled by unit Walk and, as there is no ground contact, by unit Swing. Several hypotheses have been discussed concerning the swing movement as such, either as a property of the swing controller with negative feedback that may overshoot the target position if no ground contact has been found followed by a back swing [15], or an intrinsic central oscillatory system implemented in the swing controller [17]. Another model [18] showed that simulation of active reaction could also produce searching-like oscillations. Berg et al. [19] could show that the non-spiking interneuron I4 seems to control search movement (for a discussion, see [20]). As, however, details are not known yet, we did not implement a specific version in neuroWalknet.

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