Neuroethology, Computational

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or plasticity may itself give rise to new or improved adaptive behaviors, but there are many cases of adaptive behaviors which are genetically determined (e.g. "hard-wired" behaviors such as reflexes and instincts).

In the context of adaptive behavior research, it becomes clear that the neural system is one component in the *action-perception cycle*

This should not be mistaken for an

than accuracy for two reasons highlighted by Arbib's work:

> "...Focusing only on components can lead one to overlook emergent effects of cooperative computation; and working with complete models, even if wrong in detail, nonetheless provides us with analytical tools applicable to future data and future, more accurate models... I think the reasons to push for completeness go beyond these, however, and reveal a further source of the value of Arbib's work for cognitive science.
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> "...[In 1978, Dennett] proposed that one approach the complexity of humans by looking at simpler systems, first solving cognitive problems as they arise in these 'simple minds' and then bootstrapping towards increasingly complex and human like cognizers. Two sorts of systems appealed to Dennett

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P. computatrix was inspired by biological data, but was not intended as a biological model. The various behaviors were generated by heterogeneous neural networks. The neuron model employed by Beer was more faithful to biology than many of the "formal neurons" used in connectionism: the units involved differential equations modelling membrane potentials, which gave his model neural assemblies a rich intrinsic dynamics. For further details, see Beer's article "Locomotion, invertebrate", in this volume.

The primary focus was on designing architectures for such units that could act as controllers for the various behaviors that *P. computatrix* should exhibit. Thus there was no treatment of learning in the initial body of work on the cockroach. More recently, Beer has reported on work which extends the original *P. computatrix* simulation model, testing it by allowing it to control walking in a real hexapod robot (Beer et al. 1992).

In the physical implementation, the control network was still simulated (i.e. the units in the neural network were not realised physically) but the sensorimotor connections to the artificial neural network were interfaced to physical sensors and actuators by means of analogue-digital and digital-analogue converters. Beer reports that in all cases, the response of the physical robot was quite similar to that previously observed in simulation. The implementation did however reveal one problem in the controller which had not been examined in the simulation. This problem (involving disturbances in the crossbody phasing of the legs) was easily rectified, but nevertheless this demonstrates that simulation models cannot be trusted as *perfectly* replicating any physical implementation they may ultimately be intended for.

3.3 The Computational Hoverfly

In studying issues in active vision gaze control with spatially variant 'foveal' sampling, Cliff (e.g. (Cliff, 1992)) constructed a simulated embedded agent whose environment and optical system were inspired by studies of the hoverfly *Syritta pipiens*. The computational hoverfly (known as *Syritta computatrix*, or SyCo for short) was a simulated agent existing in its own 'virtual reality'.

SyCo replicated (at the behavioral level) the visually guided tracking movements made when male *S. pipiens* pursue conspecific flies in the hope of finding a mate. The network processing model was based on previously untested models proposed in the biology literature by Collett and Land (1975).

In the SyCo simulator, a dynamic 3D world model of the relative positions and orientations of SyCo and a number of 'target' flies was used to synthesize visual input, via an accurate model of the optical anatomy of male *S. pipiens*. Within the simulator, the visual input was passed through parallel image-processing networks which effected crude target-identification mechanisms (cf. 'bug-detectors'); the results of this process were fed to tracking networks based on proposals by Collett and Land. The output of the tracking networks could alter the position and orientation of SyCo within its simulated world. The positions and orientations of the target flies could also vary dynamically, and the positions and orientations of the objects in the model were further varied by perturbations which model noise in effectors and crosswinds or turbulence in the air.

The simulation studies revealed opportunities for correction and extension of the prior models: simulating a proposed model enforces a degree of mechanistic rigour which is highly likely to expose any shortcomings or discrepancies in the model. For example, constructing the SyCo simulation required a more accurate characterisation of both the optical data, and of the fly's interaction with its environment (Cliff, 1992), than was previously available in the literature. Furthermore, experience with simulating the original proposed model suggested alternative

with the execution of behavioral outputs governed by a centralized "command center" (e.g. a 'command neuron'); instead, distributed heterarchical decentralized control systems with inputs and outputs at many levels have been proposed as better accounting for the interaction between sensory input, central pattern generation, and behavioral output, in locusts, cats, and frogs.

4 DISCUSSION

Computational neuroethology studies neural mechanisms which generate adaptive behaviors, and hence requires that agents are studied within the context of their environmental and behavioral niches.

From the above descriptions, some patterns emerge: all of the CNE projects mentioned are dependent on the availability of fairly detailed neuroethological data. Such data invariably comes from invasive *in vivo* experimentation, and the neuroanatomy of 'lower' animals such as arthropods is particularly amenable to such techniques: certain neurons performing particular functions are readily locatable in different individual animals of the same species. There are manifest obstacles preventing the collection of such data from human subjects. Furthermore, by definition, any truly *general* principles underlying the neural generation of adaptive behaviors are those which are common to a number of species, so only cross-species studies will help identify general principles (Cliff, 1990, p.37).

Most of the CNE projects have largely eschewed the study of learning (plasticity), postponing study until sufficient knowledge of the architecture of primary sensory-motor pathways is known to clearly understand how plasticity might increase the capacity for generation of adaptive behavior: cf. (Beer, 1990, p.62); so far, the design approach has had much to offer.

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