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*Adaptive Behavior* 2009; 17; 343

DOI: 10.1177/1059712309340861

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## Do Animat Models Always Need a Biological Target Organism?

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In her target article Barbara Webb reviews the relevance of animat research for answering questions in biology. Webb draws a strict line between models that target a particular organism, such as her own work on cricket phonotaxis, and more conceptual models that mainly consider invented agents, which is exemplified by the work of Beer (2003). Here, I want to address four of Webb's major considerations about animat models: their generality, their strength for generating novel hypothesis, their realism, and their lack of a target organism.

In my opinion the most important question raised in Webb's article is whether or not animat models are general, a claim often made by researchers conducting animat research. Webb points out that too often animat models fail to explain many specific biological systems. Referring to her own work she admits that her model is probably also not very general. It is an abstract representation of a neural circuit based on data obtained from experiments on the phonotaxis of real crickets. However, I agree with her that in contrast to most animat models her model may be much easier to test for its generality, simply because it is much more straightforward to design follow-up experiments with the real animals.

I also agree that abstraction does not imply generality. Most animat experiments in the realm of Beer's work represent one very specific system that usually has a very specific sensorimotor setup, control structure, and environment. Agents in those models are abstract seen from a biological perspective, but they are never-

theless very specific. However, Beer's work also shows us how we should approach animat research, that is, by thoroughly analyzing every detail of the obtained behavioral mechanisms. Too often, not even this step is taken and analysis remains rather qualitative on a behavioral level. Only if we fully understand our artificially generated systems, we can judge their value. In the case of Beer's work, I believe we have learned a lot, especially from a methodological point of view, that is, how to apply dynamical systems theory to understand the neural mechanisms of various different behaviors (Hülse, Wischmann, Manoonpong, von Twickel, & Pasemann, 2007). One of the pioneers of cybernetics, Grey Walter, has taught us how simple machines with simple mechanisms can display seemingly complicated behaviors (Walter, 1953). With the rise of behavior-based robotics we learned more about the importance of embodiment and situatedness (Brooks, 1999). Most of the work done in those fields corresponds to Webb's definition of animat research. Thus, I believe animats have been, and still are, very useful, in particular for what Webb refers to as "pure exploration." However, I agree with Webb that most of those models are not general. Principles found in one particular system do rarely hold for other systems and, most importantly, almost no comparative experiments are done. But I do not believe that the main problem is that those models have no specific biological target organism in mind as argued by Webb.

Take for instance the highly general model of the evolution of social behavior developed by Hamilton

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(2009), Vol 17(4): 343–345.  
DOI: 10.1177/1059712309340861

(1964). His famous rule  $rb > c$  states that altruistic acts become evolutionarily stable if the relatedness between receiver and actor ( $r$ ) multiplied by the reproductive benefit gained by the receiver through this act ( $b$ ) is higher than the reproductive cost caused by the altruistic behavior to the actor ( $c$ ). So far, this simple rule has proven useful to explain altruism in almost all social animals. Only recently did it become feasible to experimentally test this rule. For instance, Diggle, Griffin, Campbell, and West (2007) were able to modify each of the three parameters in bacterial populations although the original model was not designed having bacteria in mind.

If we accept Hamilton's model to be of general nature, then it should also hold for invented creatures. As just one example, Waibel (2007) showed that indeed Hamilton's general model explains the evolution of cooperation in groups of robots that were chosen rather arbitrarily, not based on any specific biological organism. This provides further evidence for the generality of Hamilton's rule. It is this *justification* value of doing animat research that I miss in Webb's analysis. Of course, we must be careful when an animat experiment fails to support a general biological theory (even though this might appear to be the more interesting experiment). But if it does, the beauty of artificial creatures is that through thorough analysis we should be able to figure out exactly why it fails. And if, and only if, this leads to precise suggestions for further experiments with animals, animat models may become a valuable tool to test, and maybe even to revise, existing biological theories. That is where I see the crux with many current studies in what Webb defines as animat research. Too often, apparently interesting results do not lead to a specific hypothesis allowing direct testing with biological organisms. From this point of view the approach suggested by Webb promises to be more successful. As an example, she briefly mentions that her experiments indicate that crickets should show certain song preferences and that particular neural connectivity structures should be found. Unfortunately, it is not revealed how far those hypotheses could be supported or contradicted with experiments on real crickets.

The generation of novel hypotheses is indeed one of the main objectives often mentioned by animat researchers and also by Webb herself. I agree with her that most research on animat models fails to provide a precise enough hypothesis that can be tested empirically on real biological systems. Often this is the case

because they were built around existing hypotheses instead of being a source model. In that respect Webb's approach may be more fruitful. But again, I disagree that the only way out is to build models of real animals. In this regard, I think much can be learned from the individual-based modeling movement in ecology and evolution (DeAngelis & Mooij, 2005; Grimm, 1999) that often shows striking similarities with many animat studies. Such models complement the classical analytical approach by putting strong emphasis on life-cycle dynamics, spatial and temporal constraints, individual variability, and resource dynamics. However, often the questions asked there are much more precise than those we typically find in what Webb refers to as animat research. For instance, with an artificial life model Hemelrijk (2000) challenged the selfish herd theory proposed by Hamilton that argues that centrality of dominant individuals in a herd as a safety mechanism can be explained by a centripetal instinct of those individuals. No such instinct has ever been found in animals. Hemelrijk's model showed that such centrality arises as a side-effect of simple self-reinforcing mechanisms of winning and losing dominance fights. This model did not target one particular organism but rather a phenomenon found across different species.

The agents in Hemelrijk's model correspond to what Webb labels *idealized* in contrast to more *realistic* biological models, exemplified by her own research on cricket phonotaxis with a robotic model. As a consequence of pursuing such realism Webb proposes to implement neural networks that resemble what is known from the cricket neural circuit as closely as possible. I am not entirely convinced that such a high degree of realism, especially on the single neuron level, is really required.

Of course, the choice of the level of abstraction always depends on the specific question one wants to investigate. In Webb's example, the studies are concerned with the neural realization of phonotaxis in crickets. I agree that in this case the connectivity between neurons is an important aspect and should be modeled as closely as possible to the real organism. Webb argues that such realism is also required on the single neuron level leading her to an implementation of a more specific neuron model. However, I have the suspicion that such an attempt to increase realism entails a certain danger. Often the data, on which those models are based, come from experiments with single individuals

or are the average over many individuals. The review of Marder and Goaillard (2006) provides many examples of the variation that can occur among individuals of one species on the single neuron level and even on the circuit level. Most remarkably, Prinz, Bucher, and Marder (2004) could generate about 20 million different models of the network that generates the pyloric rhythm of the crustacean stomatogastric ganglion resulting in almost indistinguishable network activity. So, it may well be that Webb's model resembles the neural activity and behavior involved in crickets' phonotaxis. However, to what extent the hand-designed network generally corresponds to many individuals of one particular cricket species is yet still to be shown. Such experimental verification becomes crucial if conclusions from this artificial model are drawn about the biological mechanisms.

In conclusion, I partially agree with Webb that many animat models would gain in relevance if they would be more grounded on data obtained from biological systems. But I do not believe that it is always necessary to have one specific organism in mind. Instead, I am convinced that, as Jacob (1977) wrote, "asking general questions [leads] to limited answers, asking limited questions [turns] out to provide more general answers." Thus, pursuing more precise questions and generating hypotheses that can realistically lead to tests in animal experiments should also make the animat approach much more relevant to biological research even without the constraint of focusing on one particular organism.

## Acknowledgments

I would like to thank Sara Mitri and Peter Dürr for their useful comments. The work of the author is supported by the Swiss National Science Foundation.

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