Inspiration, simulation and design for smart robot manipulators from the sucker actuation mechanism of cephalopods

Frank W Grasso and Pradeep Setlur¹

BioMimetic and Cognitive Robotics Laboratory, Department of Psychology, Brooklyn College, The City University of New York, 2900 Bedford Ave, Brooklyn, NY 11210, USA

E-mail: fgrasso@brooklyn.cuny.edu

Received 1 August 2007 Accepted for publication 10 August 2007 Published 16 October 2007 Online at stacks.iop.org/BB/2/S170

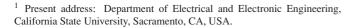
Abstract

Octopus arms house 200-300 independently controlled suckers that can alternately afford an octopus fine manipulation of small objects and produce high adhesion forces on virtually any non-porous surface. Octopuses use their suckers to grasp, rotate and reposition soft objects (e.g., octopus eggs) without damaging them and to provide strong, reversible adhesion forces to anchor the octopus to hard substrates (e.g., rock) during wave surge. The biological 'design' of the sucker system is understood to be divided anatomically into three functional groups: the infundibulum that produces a surface seal that conforms to arbitrary surface geometry; the acetabulum that generates negative pressures for adhesion; and the extrinsic muscles that allow adhered surfaces to be rotated relative to the arm. The effector underlying these abilities is the muscular hydrostat. Guided by sensory input, the thousands of muscle fibers within the muscular hydrostats of the sucker act in coordination to provide stiffness or force when and where needed. The mechanical malleability of octopus suckers, the interdigitated arrangement of their muscle fibers and the flexible interconnections of its parts make direct studies of their control challenging. We developed a dynamic simulator (ABSAMS) that models the general functioning of muscular hydrostat systems built from assemblies of biologically constrained muscular hydrostat models. We report here on simulation studies of octopus-inspired and artificial suckers implemented in this system. These simulations reproduce aspects of octopus sucker performance and squid tentacle extension. Simulations run with these models using parameters from man-made actuators and materials can serve as tools for designing soft robotic implementations of man-made artificial suckers and soft manipulators.

(Some figures in this article are in colour only in the electronic version)

1. Background

Cephalopod mollusks (nautiluses, cuttlefishes, squids and octopuses) are soft bodied organisms that manipulate objects in their environment with a sophistication that is comparable to that of higher vertebrates (Hanlon and Messenger 1996). Octopuses, for example, can open jar lids to capture crabs inside transparent bottles (Fiorito *et al* 1990) and arrange



stones and seashells to enhance the protective value of den entrances (Mather 1994). The parts of cephalopod bodies that effect manipulations are built, surprisingly, without hard parts. In contrast to arthropods with an exoskeleton and vertebrates with an internal skeleton upon which muscles work, cephalopod bodies are composed almost entirely of muscle and flexible connective tissue (Kier and Smith 1985).

The general biomechanical principles for this class of actuation in cephalopods are well understood (Kier and Smith 1985). Muscular hydrostats (MH) (Kier 1988) are

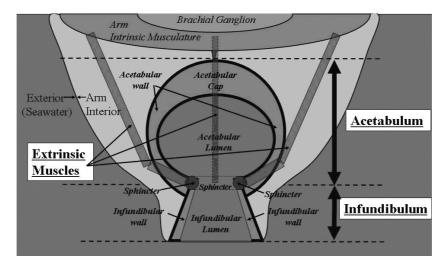


Figure 1. Schematic illustration of the major components of an octopus sucker. This figure represents a vertical cross-section through the middle axis of the radially symmetric structure. Interior lumens are shown in medium gray, the arm in light gray, structural elements of the sucker in darker grays. In the octopus sucker extrinsic muscles run between sphincter and arm connective tissue in a continuous, conical sheet; in this diagram only three extrinsic muscles are shown to illustrate the connectivity. Typical octopus sucker diameters (across the acetabulum) range from just under a millimeter at the tips of the arms of pacific giant octopuses to over 8 cm toward the base of Pacific Giant Octopus arms (see Voight (1993) for the range of octopus sucker parameters).

constituted of muscle fibers, cellular organelles and interstitial fluid that are within enclosed compartments and therefore subject to a constant volume constraint. The enclosed muscle fibers are not all arranged in parallel as seen in arthropod and vertebrate skeletal muscle; rather the muscle mass can possess interdigitated fibers at several, often perpendicular, orientations. A contraction of the enclosed muscle fibers in one direction must produce an expansion of the muscular hydrostat in another in order to satisfy the constant volume constraint. Thus, activated groups of muscle fibers at one orientation can act as antagonists to muscle fibers arranged at other orientations and result in a change in the muscular hydrostat's shape. The muscular hydrostat is conceptualized as a bounded continuum of fluid (since the components have a density that is comparable to water) with the capability to reshape itself arbitrarily through the selective contraction of subsets of the muscle fibers contained within. As Kier and Smith (1985) pointed out, this is distinct from the hydraulic mechanisms of hydrostatic skeletal systems such as those in sea stars. In hydrostatic skeletal systems fluid moves from one compartment to another under pressure produced from force generating elements that lie outside the compartments. The result is stiffening throughout the structure which can be likened to human engineered pneumatic and hydraulic actuators. Because muscular hydrostats consist of a single compartment containing muscle rather than free-flowing fluid, local contractions of muscle fibers inside muscular hydrostats produce local stiffening of the hydrostat and local force generation. Thus, in contrast to a hydrostatic skeleton, the muscular hydrostat contains both active stiffening and force generating elements capable of localized action (for review see Kier and Smith (1985)).

Not surprisingly, cephalopod muscular hydrostat systems led several robotics researchers interested in 'continuum robotics' (soft robots) to study muscular hydrostat systems like the octopus arm or elephant trunk for design insights and operational principles (Walker 2000, Hannan and Walker 2003, Walker *et al* 2006, Robinson and Davies 1999). Cephalopod muscular hydrostat systems are distinct from natural and man-made hydraulic or pneumatic systems in which fluid from one enclosed region is induced by pressure to move, deflate or inflate a distant region. Numerous units without the need for long fluid-supply lines offer the potential for great local flexibility. They are also examples of hyperredundant systems, systems with excessive degrees of freedom. These are desirable in robotics systems for their properties of graceful degradation² of function with damage and ability to operate in cluttered environments (Walker *et al* 2006).

Octopus suckers are unique manipulation devices and may be the most structurally complex organ to which cephalopod muscular hydrostats have been applied. Octopus suckers are radially symmetric structures suspended from the oral surface of the octopus arm that incompletely enclose a volume of ambient fluid; seawater for an octopus in the ocean or air for an out-of-water octopus. It is the ambient fluid medium that the sucker acts upon to reversibly attach an object to the octopus arm or the octopus arm to a surface. The mechanisms by which they facilitate grasping in octopus have been inferred from anatomy (Kier and Smith 2002) and their force generation capabilities have been studied in the laboratory (Smith 1996). The three functional components are referred to as the acetabulum, infundibulum and extrinsic muscles (figure 1). The muscular hydrostat elements in the infindibulum reshape the sucker rim to conform to the exterior surface. Once a seal is formed the acetabulum produces negative pressure

 $^{^2}$ Graceful degradation is a property of systems with multiple redundancies, such as the systems of muscular hydrostat units described here. In such systems the failure of a subset of components leads to gradual decrease in performance rather than system failure. This is in contrast to 'brittle' systems in which the loss of one component leads to the total performance failure of the system.

(and therefore adhesion force) by reshaping itself to virtually³ expand the small, enclosed fluid volume. The fluids enclosed in the acetabulum and infundibulum communicate through a narrow muscular sphincter, so the fluid in the infundibulum, when the sucker is unattached, is continuous with the ambient fluid. With the surface held, the extrinsic muscles are arranged so that they may act in antagonistic pairs to rotate the surface relative to the arm. In water, these three major anatomical components and associated connective tissue act to control fluid within the lumen to produce up to 2 atmospheres of pressure relative to ambient and enormous adhesive force (Kier and Smith 2002).

Three published computer models that describe the dynamics of cephalopod appendages take different approaches to modeling muscular hydrostat systems. Gutfreund et al (1996) quantitatively studied the reaching movements of the octopus arm upon which Yekutieli et al (2005) formulated an elegant, biologically constrained model, which used dynamic stiffness control as the means of muscular hydrostat action. Individual muscle fibers or functional groups of muscle fibers were not represented in this model; rather cross-sections of the arm were modeled as point masses connected by springs. A finite element formalization of this type of continuum approach to modeling muscular hydrostat systems was developed by Liang et al (2006), which introduced a richer diversity of component shapes in a computationally convenient environment. This latter model was validated, as was the modeling system presented here, based on quantitative data on the squid tentacle extension rather than octopus arm movements. In the limit, an infinite number of sections would form a continuum that quantitatively captures biologically observed reach in the octopus as a mechanism of arm extension as stiffening waves initiated at the arm base and propagating down its length toward the tip. Van Leeuwen and Kier (1997) using an approach similar to that we present here, modeled explicit, idealized, muscular hydrostat elements, that they called 'disks', in a one-dimensional array to capture the dynamics of squid tentacle extension. In this model, the action of muscle fibers within the disks was modeled by contraction in a single direction to extend the tentacle in a perpendicular direction. This model succeeded in explaining the functional consequences of muscle biochemistry for aggregates of fast specialized muscle fibers contained in the squid by quantitatively reproducing the dynamics of tentacle extension.

A feature of cephalopod muscular hydrostats that is implicitly captured in these models is that not all of the muscle fibers, even those arranged in parallel are necessarily activated at one time. We capture this aspect explicitly in our modeling system. The motor neurons that activate muscle fibers within a muscular hydrostat can activate subsets of these muscle fibers for differential control. In our modeling of biological muscular hydrostat systems we use a concept

from neurobiology to introduce the concept of the muscular hydrostat unit (MHU). In the late 19th century, Sherrington introduced the term motor unit to refer to the motor neuron in the spinal cord [in vertebrates] and the population of muscle fibers that it inervates (Kandel et al (1991), p 15). The arrangement of nerve fibers and neuromuscular junctions inside cephalopod muscular hydrostats, and the observed local action of muscle fibers contained within the muscular hydrostats of live cephalopods indicates the existence of a parallel basic physiological unit. In this paper we use the term muscular hydrostat motor unit, when we wish to refer that subset of muscle fibers within a cephalopod muscular hydrostat that is activated by one motor neuron. Today we do not know whether the vertebrate principle of each muscle fiber being controlled by a single motor neuron applies in cephalopods so we apply the motor unit concept loosely in the modeling results reported here. We use the term *muscular* hydrostat unit (MHU) in this paper to refer to those units that are simultaneously activated within a muscular hydrostat model through a single activating command. The muscular hydrostat unit, in the simulations presented here is not a oneto-one model of a muscular hydrostat motor unit. Rather, they represent the hypothesized actions of functional groupings of muscular hydrostat motor units. This approach is useful in modeling muscular hydrostat systems by allowing us to explicitly represent the activation of antagonistic subsets of muscle fibers within a muscular hydrostat.

In our modeling approach, geometry changes in one muscular hydrostat unit can cause the displacement in adjacent muscular hydrostat units to which it is mechanically attached or with which it collides. Changes in multiple muscular hydrostat units can reshape an entire anatomical structure: a bend in an octopus arm can be produced by lengthening the muscular hydrostat units on the surface of the arm exterior to the bend and a shortening (perpendicular contraction) of those on the interior (Kier 1988). The muscular hydrostat units in a cephalopod appendage are attached with connective tissue, the stiffness of which is varied from location to location, limiting the degrees of freedom in the motions of assemblies of muscular hydrostat units. Thus, connective tissue can be thought to channel the geometry changes in the appendage as a whole. This is particularly relevant to the modeling of suckers as will be seen below.

In continuum models of cephalopod muscular hydrostat systems that aim, such as those described above, to capture aspects of cephalopod arm motion, the aggregate motion of the larger structure is the goal, the action at the boundaries between the individual muscle fibers and the local geometry of force generation are not explicitly modeled. In octopus suckers the arrangements of muscle fibers and connective tissues are spatially complex. Further, the anatomical structure of the sucker suggests that several parts (such as the infundibulum and the acetabulum) act as independent muscular hydrostats. In this situation, where muscular hydrostat units and connective tissues are arranged in a multitude of oblique orientations, the interactions at the boundaries of the functional groups are likely to be important and a discrete, rather than continuum model, that captures some of these anatomical

³ We use the word 'virtually' here because the actual volume change observed in octopus suckers is so small as to be negligible. The high bulk modulus of water requires a tremendous application of force by the sucker walls to produce a volume change. The net result is high negative pressure without visible change in the lumen volume of the acetabulum. See Smith (1996) for detailed discussion.

structures may be more appropriate. It will certainly yield different insights and provide complementary information. This is particularly true if small numbers of units that do not approach the continuum limit are to be employed for computational tractability (i.e., our functional approach to modeling muscular hydrostat motor units as muscular hydrostat units). The discrete approach also has the advantage that the parts are in one-to-one correspondence with parts that may be fabricated for a robot implementation: the simulation becomes the blueprint.

In our approach, we have modeled a collection of discrete interacting muscular hydrostat units similar to those modeled by Van Leeuwen and Kier (1997). In the modeling environment we report on here we use standard techniques from computational geometry to extend this 1D discrete approach to allow 3D arrangements of functional muscular hydrostat units in space with arbitrary sizes, positions and orientations. We also explicitly model the properties of connective tissue in 3D space to constrain the collective actions of the muscular hydrostat units as they are constrained in biological systems. A core aim of this software system is to serve as both a test-bed for studying the control of muscular hydrostat unit systems and as a prototyping system for designing robot implementations composed of artificial actuators that emulate the desirable properties of muscular hydrostat units.

2. Approach

We began our development of muscular hydrostat unitinspired sucker robots with the development of a computer software package: the Artificial and Biological Soft Actuator Manipulator Simulator (ABSAMS). The simulator models individual muscular hydrostat units as objects that can change shape by shortening along one dimension while maintaining constant volume. This shortening is modeled, as detailed below, as an application of force along one dimension. Though ABSAMS supports other shapes, for the simulations reported here the units are all cylinders that maintain cylindrical geometry when a forcing function is applied. Thus in a cylindrical ABSAMS MHU, a contraction along the radius produces increase in length and vice versa.

The active shortening of one dimension in cephalopod muscular hydrostats is the only forcing function for geometry change because muscle fibers only produce force through When the neuron that activates a muscular contraction. hydrostat motor unit fibers, it produces a local shortening that produces a tension in the surrounding tissue. When that neuron stops firing the muscle fiber within it no longer supplies an active force to hold the shorter length and the passive stiffness of the surrounding muscle and connective tissue re-lengthens the muscular hydrostat motor unit to equilibrate the tension in the tissue. This is a relatively slow process, compared with muscular contraction. This is captured in ABSAMS (see below) as well as the faster process of activation of antagonistic muscular hydrostat units. Within a single muscular hydrostat, multiple sets of non-parallel muscle fibers that can produce antagonistic forces also result in a restorative shape change. For example, within a cylindrical muscular hydrostat two muscular hydrostat units may produce antagonistic shortening if one is oriented along the radius and the other along the length of the cylinder—two muscular hydrostat units within each cylinder act in opposition. The activation of the antagonists in the model could be used, as it is in vertebrate systems, to quickly return the system to a position suitable for initiating a sucker adhesion cycle.

However, for the modeling described in this paper neither the use of antagonists nor the passive return was central to the results obtained. We implemented, in broad outline, the mechanism of sucker adhesion described by Kier and Smith (2002). Since Kier and Smith's proposed mechanism was based on anatomical considerations the modeling studies reported here become a means of studying dynamics of their mechanism. Our arrangement of muscular hydrostat units in the model (detailed below) produced sucker attachment with a sequence of MHU activations that followed the broad outline Kier and Smith described without involving antagonist muscle units. Further, the production of adhesion did not require the inactivation of activated units; units once activated remained activated while adhesion was maintained. Thus, the modeling results presented here result from a relatively simple control mechanism for a manipulator with a complex physical structure.

We made two simplifying assumptions in the implementation of the muscular hydrostat units that differ from the known physiology. Our muscle fibers produce a constant force (tension) at all lengths where real muscle fibers are well known to possess 'j-shaped' force-length relationships. Similarly, the resistance of our model muscular hydrostat units to deformation is also linear whereas in real muscles the relationship is nonlinear. We used values for these constants that were derived from the literature and scaled them appropriately for the sizes of our muscular hydrostat units. These assumptions mean that the dynamics of response in our muscular hydrostat units will differ in detail, but probably not in aggregate, from biological muscle. These features could have been included in the model (and may be in future ABSAMS implementations) but we decided that the analysis of sucker model dynamics and translation to robot implementation would be simplified with these linear assumptions.

Groups of muscular hydrostat motor units in cephalopods are held together by fibrous connective tissues that serve to channel and restrict the actions of the muscular hydrostat units. The simulated muscular hydrostat elements (cylinders) are connected by simulated connective tissues (combinations of linear springs and dampers) attached to arbitrary points on pairs of muscular hydrostat elements. We call spring attachment-points nodes. Nodes are fixed points on the surfaces or fixed points inside muscular hydrostat units that maintain proportional distances from the center of the muscular hydrostat unit as the muscular hydrostat unit changes shape. Nodes translate through space with the motions of the muscular hydrostat units to which they are attached⁴. Nodes

⁴ Nodes may also be 'anchor nodes' which are not fixed to points on MHUS but rather are fixed to specific points in the simulation space. Such nodes are immovable and are used to anchor the simulated assembly in space.

Table 1. Some constants	s used to constrain	n the	simulations.
-------------------------	---------------------	-------	--------------

Quantity	Value	Reference
Cephalopod muscle force/unit area	600000 N m^{-2}	Kier and Curtin (2002)
Cephalopod muscle density	1000 kg m^{-3}	Kier and Curtin (2002)
Collagen damping	10 N s m^{-1}	Determined in the simulation
Rubber damping	10 N s m^{-1}	Determined in the simulation
Connective tissue stiffness ^a	$7.0 \times 10^{6} \mathrm{N} \mathrm{m}^{-1}$	Faulkner et al (1968)
Rubber stiffness	$7.0 \times 10^{6} \mathrm{N}\mathrm{m}^{-1}$	Weast (1976)
Bulk modulus of water	$2.35 \times 10^{9} \text{Pa}$	Weast (1976)
Passive muscle stiffness ^b	900000 N m^{-2}	Kier and Curtin (2002, figure 6)
Radial muscle stiffness	$5.0 \times 10^4 \text{ N m}^{-1}$	Calculated from passive muscle stiffness
Longitudinal muscle stiffness	$1.23 \times 10^4 \text{ N m}^{-1}$	Calculated from passive muscle stiffness
Muscle damping	1200 N	Determined in the simulation

^a In the biological literature stiffness is expressed as Young's modulus with units of N m⁻². ABSAMS represents connective tissue and muscle action in one-dimensional, point-to-point links. For this reason the stiffness used in the simulation is linear stiffness in the sense of Hooke's law for springs. ^b Kier and Curtin report the passive stiffness of squid arm muscle bundles as 1.5 times the peak twitch they observed in their studies. We have used this factor and their reported twitch to calculate the 900 000 N m⁻² we used in the simulations. Radial and longitudinal muscle stiffness, listed below, were calculated from this value as a one-dimensional stiffness based on the geometry of a simulation MHU. The values calculated for a nominal cylindrical MHU with a radius of 1 cm and a length of 2 cm were used throughout the simulation.

may connect to any number of springs but springs only connect two nodes and we place no limit on the number of nodes that can be attached to a given muscular hydrostat unit.

When two nodes are pulled apart, the spring connecting them acts to resist movement following a simple onedimensional (Hookeian) proportional stiffness. This resistive force is applied to the muscular hydrostat units at the point of attachment. The force is applied at the node in a direction that is parallel to the line connecting the two nodes in space. A system of muscular hydrostat units, springs and nodes constitutes a muscular hydrostat unit 'assembly' that might represent a single muscular hydrostat or a set of attached muscular hydrostats.

Shape changes in one muscular hydrostat unit can produce translations in adjacent muscular hydrostat units by collision and by force transmission between muscular hydrostat units connected by springs. Thus, as in biological muscular hydrostats, the action of a single muscular hydrostat unit in ABSAMS can potentially reshape the entire assembly. Coordinated action of many muscular hydrostat units can produce reshaping of the entire structure subject to the muscular hydrostat unit constant volume and connective tissue (spring) constraints. The ABSAMS simulation system, with appropriate parameters and assembly geometry is thus a tool to explore various types of muscular hydrostat unit assemblies, such as the sucker modeled here.

Control over a muscular hydrostat unit assembly is exerted through commands to individual muscular hydrostat units (i.e., the motor unit concept). Each muscular hydrostat unit command directs the contraction along one dimension in a single cylinder. This is consistent with biological muscular hydrostat units in which muscle fibers run only in one direction⁵. Each can be independently activated by an input in the interval [0, 1]. A value of 1 indicates maximal activation. The ability of cephalopod muscular hydrostat units to produce graded force and transformation is captured by using a variety of values in this range; however, for the simulation results reported here only binary activations (i.e., 0 or 1) were used for simplicity.

The ABSAMS simulations we report were well constrained to material properties and only two damping parameters were estimated. Forces of gravity and buoyancy are explicitly included to act on each muscular hydrostat unit. Forces arising from collisions between muscular hydrostat units in dynamic simulation were resolved according to Newtonian mechanics using the SOLID software package (Van Den Bergen 2004). The physical constants for the properties of the springs and muscular hydrostat units were taken from published literature values. The more obscure ones are listed in table 1. Since measures of damping at the fine tissue level were not available from the literature these were determined empirically from the model to produce smooth dynamics free from oscillations. (This issue will be treated in detail in the discussion.)

Finally, the simulation environment is an interactive tool that uses the Open-GL software library (Shreiner 2000) to render the progression of muscular hydrostat unit assembly states in 3D graphics. A graphical user interface makes it possible to adjust parameters, insert, delete or reposition muscular hydrostat units, add, delete or reconnect springs. It also includes visualization tools that examine the graphical representation of the state of the muscular hydrostat unit assembly using zoom, rotate, pan and tilt, and interrogate the state of a given muscular hydrostat unit. These tools proved quite valuable in analyzing and refining assembly designs.

2.1. Validation of the model system

2.1.1. Individual MHUs. We used the ABSAMS system to construct and control single muscular hydrostat cylinders

⁵ In the ABSAMS environment separate commands can be delivered to the perpendicular fibers within the MHU. This was not necessary for the simulations reported here and all commanded MHU activations were along a single dimension.

in isolation (i.e., without connecting them to other muscular hydrostat cylinders). Such single unit 'assemblies' permitted us to evaluate the reasonableness of the dynamics in the basic simulation component free from the complications of a full assembly of muscular hydrostat units. We instantiated these single muscular hydrostat cylinders at over a range of biologically reasonable sizes: from lengths and widths less than one millimeter to several centimeters. We then activated them and recorded the time to 99% asymptotic size change. The range of values obtained varied from 100 to 1500 ms. This range reasonably matches the range of values for contraction times observed in cephalopod muscle. We note that these dynamics emerged from model MHUs that were constrained by measured biological constants and derived from first-principles. We interpret this to mean that the model muscular hydrostat units provide a reasonable first approximation of cephalopod muscular hydrostat motor unit dynamics in situ. The further implication of this is that the shape changes in the model MHUs reasonably match those of their biological analogs. This is particularly important because it indicates that the simplifying assumptions about muscle stiffness and connective tissue (spring) stiffness discussed above did not produce reshaping dynamics that were on an inappropriate scale. More detailed modeling will undoubtedly produce differences, potentially important differences, in performance detail but for the time being we believe we have a reasonable first approximation.

2.1.2. Assemblies of MHUs. The numerous parts and complexity of the sucker muscle geometry make collection of quantitative performance data on the action of individual muscular hydrostat motor units in situ exceedingly difficult, if not impossible. No quantitative data are available today. As an alternative to direct measurement in suckers we turned to a simpler muscular hydrostat unit system for validation of our assembly approach. Squid tentacle extension for prey capture is a well-studied behavior that has been described kinematically with high-speed video (Kier and Van Leeuwen 1997) and modeled quantitatively (Van Leeuwen and Kier 1997). We modeled the squid tentacle an assembly of 13 cylindrical muscular hydrostat units oriented with their long axes along a single line and connected end to end with springs. Squid tentacles' rapid response depends on a specialized fast muscle fiber so the muscle force-generation properties were adjusted in these simulations from octopus to squid tentacle muscle fiber (Kier and Curtin 2002). The velocity profiles of our activated assemblies agree quantitatively with both the squid kinematics and the previous modeling effort. We take this as evidence that ABSAMS is able to model the dynamics of cephalopod muscular hydrostat unit systems to a reasonable first approximation.

2.2. The sucker model

2.2.1. Components of the model sucker assembly. The first implementation consisted of a 1 cm diameter octopus sucker. This is on the large size of typical suckers, which range from less than 1 mm in pygmy octopuses (*Octopus bocki* Adam, 1941 or *Octopus wolfi* Wülker, 1913) to about

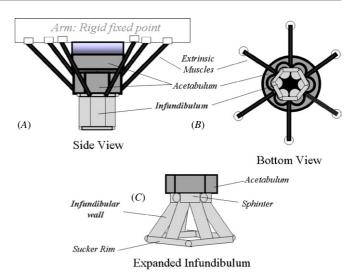


Figure 2. ABSAMS simulated artificial sucker design. (*A*) Side view of the sucker in its inactive, resting state, with parts labeled. (*B*) Bottom view of the sucker from the perspective of looking into the lumen. The arm lies behind the sucker in this view. (*C*) Side view of the infundibulum flared out for seal formation. The wall elements and rim elements are lengthened and the sphincter elements are shortened relative to (*A*). Springs are not shown to reduce image clutter. Some parts are obscured in this view. See the text for a complete list of components.

8 cm in Pacific Giant octopus (Enterooctopus dolflini Wülker, 1910). The model was composed of 39 MHUs, 139 nodes and 76 springs. These component parts represent a compromise between biological realism and computational tractability. Each of the 139 MHUs implemented represents functional assemblies (as described above) of muscular hydrostat motor units in the octopus sucker. In the biological system there are more actual muscular hydrostat motor units than we have represented. We have summarized them by representing in single muscular hydrostat units groups of muscular hydrostat motor units that are thought to work together in realizing sucker adhesion, manipulation and release of attached surfaces. The springs and nodes model, to a first approximation, the geometry of the connective tissues that constrain muscular hydrostat unit action within the sucker. A more detailed model might lead to greater biological validity but would certainly lead to a computationally more cumbersome model with possibly limited additional insight into the function of artificial or biological suckers. We refer the parts of the model sucker for their biological analogs: acetabulum, infundibulum and extrinsic muscles (figure 2). We describe the resting, inactivated state of the assembly in the paragraphs that follow.

The infundibulum was modeled using 12 MHUs. Six cylindrical MHUs were arranged in a hexagon with their long axes parallel. A volume enclosed within these six constitutes the lumen of the infundibulum through which pressure generated in the acetabulum could be transmitted to the contacted surface. A rim was constructed of six smaller MHUs arranged in a ring with their radial axes parallel. This rim was attached to ends of the MHUs that formed the wall. Both were controlled by radial contractions. A radial contraction of the rim MHUs flares out the infundibulum;

a motion produced in octopus suckers though realized with a somewhat different, more complex mechanism involving more antagonistic MHU groups. A radial contraction of the other six MHUs would cause them to lengthen and thereby extend the infundibulum away from the sucker and toward a surface.

A second ring of six MHUs above the infundibulum modeled the sphincter that lies between the infundibulum and acetabulum. These were arranged parallel to the rim MHUs and connected to the infundibular wall MHUs in the same fashion as the rim. (The infundibular wall was sandwiched between these two rings of perpendicularly arranged MHUs.) Contraction along the length of these units closes the sphincter ring and pulls the MHUs of the infundibulum wall together. This stiffening stabilizes the structure for the wall. Our earlier models of the sucker, constructed without this structure and dynamic control, were unstable. This is a consistent modeling result that deepens our understanding of the biological function of the sphincter itself. In addition, through an opposing action to the rim muscular hydrostat units, this ring of MHUs aids in flaring the infundibulum outward in seal formation.

The acetabulum was modeled as seven MHUs. Six are arranged like those of the infundibulum, and are passive elements. The seventh, large, MHU is referred to as the acetabular cap that caps the upper ends wall ends and encloses the interior volume. This unit is oriented with its long axis parallel to the wall units. Contraction along its length causes a large radial expansion that pulls the wall units away from the central axis of the sucker. The activated sphincter below anchors the lower ends of wall units to the middle axis of the sucker and provides dynamic mechanical stability. This action increases the interior volume of the acetabulum in octopus suckers and generates the negative pressure for adhesion.

Six MHUs model the extrinsic muscles that connect anchor points above with the sphincter. Contractions of these units along the length, excited as antagonistic pairs, can rotate the entire structure and translate attached surfaces through space. We also experimented with an extrinsic cap above the acetabular cap that models a diffuse mass of muscle and connective tissue that lies between the sucker and the arm of the octopus. Initial ABSAMS models, implemented with earlier sucker designs that lacked this extrinsic cap could not match the extension found in real octopus suckers. These earlier models relied on the ability of the infundibulum to expand in order to reach toward the surface to be attached. This was not found to be adequate and review of the sucker anatomy and observation of videos of octopus suckers in the process of adhesion suggested that an extension of the extrinsic cap might be a solution. Thus, the exploration with these models indicated a limitation of current thinking about sucker function and supplied evidence for a mechanism by which part of that sucker function is realized.

The remaining muscular hydrostat units, nodes and springs served anchoring functions to fix the model sucker in space in a manner analogous to it being anchored to the octopus arm.

2.2.2. *Control of the sucker model in a grasping task.* Twenty-five of the thirty-nine muscular hydrostat units in the

sucker model were activated to reshape the sucker assembly in the grasping simulations. These were divided into three functional groups that respectively implemented the operations of seal formation, adhesion generation and manipulation. The first group consisted of the six muscular hydrostat units in the infundibulum wall, the six on the sucker rim and the six that constituted the sphincter and functioned to produce seal formation. The second group consisted of the single large muscular hydrostat unit on the acetabulum cap and was used for generation of adhesion force. The final group was the six extrinsic muscles use for manipulation of the adhered surface. To realize the sucker adhesion each of these groups (infundibulum, sphincter and acetabulum cap) is activated sequentially and implemented with a separate feedback control circuit and sensors. Figure 3 summarizes the implemented control scheme in a finite state acceptor (FSA) diagram.

Seal formation is realized by the simultaneous extension of the six infundibular wall muscular hydrostat units, the narrowing of the six sphincter muscle ring muscular hydrostat units and expansion of the six sucker ring muscular hydrostat units. The narrowing of the sphincter combined with the expansion of the rim causes the sucker infundibulum to flare out (figure 3) and the lengthening of the wall muscular hydrostat units extends the infundibulum to contact any surface below and close to the sucker. The narrowing of the sphincter also provides mechanical support for the entire structure; tightening linkages between the muscular hydrostat units in upper infundibulum and lower acetabulum. The expansion of the infundibulum is under local feedback control in that it is inhibited by contact sensors of the sucker rim with an external surface. When all six rim muscular hydrostat units are in contact a seal is assumed to be formed and commands are sent to the acetabulum cap muscular hydrostat unit to realize attachment.

Following the initial activation of these units the sphincter and rim rings reach asymptotic shape more quickly than the larger wall muscular hydrostat units leaving the wall muscles to continue to expand outward from the acetabulum. In the model this quicker arrival at asymptote results from the fact that the smaller units, while employing the same force-velocity relation as large units (constrained to measured cephalopod muscle properties, Kier and Curtin (2002)), act on a smaller mass. We ran these simulations to take advantage of these features but in fact, much finer control is possible with this system. For example, lower levels of activation of smaller muscular hydrostat units could be applied to smaller muscular hydrostat units designed to allow them to arrive at asymptote at the same time or even after the larger muscular hydrostat units. These issues of control are of fundamental interest in understanding muscular hydrostat systems and can be explored in ABSAMs.

Once seal formation is signaled by the six rim units the sucker control system proceeds to generate negative pressure, relative to ambient, to attach the surface to the sucker. This is accomplished in the simulation, as it is in the octopus sucker, by an expansion of the volume within the lumen of the acetabulum. In the model a command to the acetabular cap muscular hydrostat unit causes its diameter to expand. Because this unit is attached to all six acetabulum wall

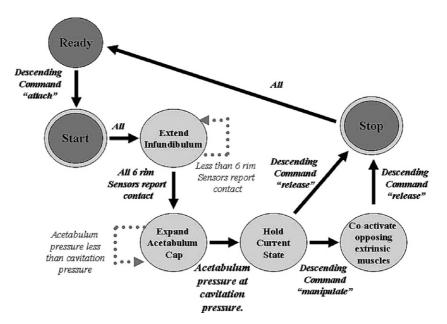


Figure 3. FSA diagram of the control scheme for the ABSAMS sucker. The main progression of the sucker control cycle appears in dark arrows. Longer periods requiring feedback control are indicated in light gray dashed arrows. The 'ready' state is the one in which the system has relaxed to its resting state. See the text for explanation of the states and transitions.

muscular hydrostat units the six muscular hydrostat units move with it. As the acetabular cap unit expands the upper ends of the wall are pulled away from the center of the sucker. At the lower end of the acetabulum the sphincter anchors the lower ends of the six acetabular wall units. The result is a net increase in the internal volume of the acetabulum.

We use this volume change to calculate the negative pressure within the lumen that this movement of the wall produces. We calculate this volume change, and the associated pressure change, by standard computational geometry techniques of Votoroni tessellation and Delauny volume calculation (O'Rourke 2005, Laszlo 1996). The acetabulum and the infundibulum are connected through the sphincter so we use the combined volume of both. We assume a minimum energy surface 'skin' covers the interior lumen that connects points on the interior muscular hydrostat unit wall surfaces. This inward pressure is applied to each muscular hydrostat unit that lines the lumen as a force normal to and proportional to its surface exposed to the lumen fluid. The same technique is used to calculate the force exerted on the attached object surface, which is the attachment force that pulls the object to the sucker rim with a force equal to that exerted by the pressure differential between the sucker lumen and the ambient fluid.

The maximum possible expansion of the acetabulum is limited by negative feedback control from the lumen pressure. Smith (1991) demonstrated that octopus suckers can generate forces sufficient to cavitate the water contained within the lumen. Thus, the realistic limit of attachment force is the pressure at which cavitation would occur. Simulated acetabulum expansion stops just below the pressure required to cavitate the fluid contained within it (-27 mPa relative to ambient (Kier and Smith 1990)). Exceeding the cavitation pressure would remove adhesion in an artificial sucker as in octopus suckers, and external forces then become necessary 'pop' suckers free from surfaces to which they are attached (Smith 1996).

With the object surface attached to the sucker, manipulation of the attached surface can proceed by antagonistic lengthening and shortening of the opposing extrinsic muscles. These muscles connect the sphincter rim to the overlying arm that is modeled as a series of fixed points in space. These movements are produced under length control of the muscles. This assumes a type of proprioceptive feedback that has not yet been demonstrated in the octopus. We will focus here on the process of attachment although manipulation abilities also have been developed for the ABSAMS sucker simulation.

2.2.3. The grasping task. Our object oriented programming approach allowed us to utilize our model muscular hydrostat cylinder and cube elements as objects for the sucker model to attach to in the simulated space. As noted above ABSAMS objects can be instantiated in arbitrary geometries: of spherical, cylindrical or 3D rectangular shapes; we can place them in arbitrary locations in the simulation space; we can specify their physical properties like density and mass. Once instantiated in the simulation space the forces applied to them by the MHU sucker assembly are resolved according to the same rules as other objects in the space for translations and rotations as a result of applied forces. As objects in the space they are passive elements of the simulation, acted upon but not acting, maintaining their base geometry throughout a given simulation.

For the grasping tasks we placed a 1 m diameter work surface in the simulation space. This was one of the flat faces of 1 m diameter cylinder of length (height) 1 cm. It was rigidly fixed in place by anchor nodes so that the collision of muscular hydrostat unit assemblies or objects would not alter its position or orientation.

We centered our model sucker over this work surface. We placed objects of various sizes and geometries directly beneath the sucker for the sucker to attempt to lift. These objects were free to translate and rotate under the action of forces applied by the artificial sucker. We placed rounded cylinders beneath the sucker to test seal formation on a curved surface and varied the radius of curvature. Naturally, the ability of the rim to match surface contour is limited by the number of muscular hydrostat units used in the sucker rim in a way that it is not limited in the octopus sucker rim. Models with more muscular hydrostat units in their rims could conform to more complex surfaces. We did not require continuous contact along the entire length of a muscular hydrostat unit which is a more realistic indicator of seal formation. We placed various rectangular objects beneath the sucker and varied their mass to test the load capacity of the sucker assemblies. The sucker was placed a height over the object that put the extended rim within the range of the object but that did not touch it at the start of a task.

3. Results

The octopus sucker model was capable of seal formation and able to attach to and lift objects under a variety of conditions. Cylinders with a radius of curvature less than the length of one of the rim muscular hydrostat units could not be sealed to the rim because the rigidity of the individual muscular hydrostat units prevented them from appropriate deformation. However, at curvatures slightly less than this, the sucker rim conformed to the curvature with little difficulty. (In alternative sucker designs, approaching the continuum limit, good mechanical seals to curved surfaces with smaller radii of curvature could be realized with rims composed of more segments than the six segments.) For curvatures approaching the length of a rim muscular hydrostat unit, the rim stretching its springs at points of stress and strain, showed a remarkable ability to passively conform: as the sucker pressed the surface complete contact by all rim units was obtained. This is an attractive property for artificial suckers and a likely mode of operation in octopus suckers.

On trials when we tested the sucker with a cylindrical object placed off-axis from the long axis of the sucker, we observed that the contact forces often translated or rotated the object into positions that further facilitate completion of the seal formation. As the infundibulum advanced downward, the points of first contact were typically with portions of the cylinder that were highest. As the sucker rim continued to advance it folded over the lower surfaces of the object. When this produced asymmetries of force the object was rotated or translated to balance these forces with the result that the object was moved to one axis of symmetry of the sucker.

Seal formation on objects that presented flat to the sucker was completely effective when the surface was horizontal as was a seal formation on surfaces with gentle tilts ($<30^\circ$) from horizontal.

Once a seal was formed, the simulated sucker was able to lift the objects via the action of the acetabulum cap and extrinsic muscles. The simulated octopus sucker could lift loads of up to 0.5 kg a distance of 5 mm and hold them indefinitely. Object loads higher than 0.5 kg produced instability in the sucker that leads to the loss of the seal and of the adhesive force. This instability has several sources that will be treated in the discussion.

Simulations with suckers of the same geometric design but scaled to a size of 13 cm showed that the ability to attach and lift objects scaled with the increased size. The larger interior infundibular cross-sections can produce greater adhesion forces at the same acetabulum-generated internal pressure. (Uniform force per unit area over a larger area is greater force.) So by scaling the size of the sucker upward, the sucker was able to lift and hold masses of about 20 kg. However, larger masses than this again caused instability that caused the sucker to lose its seal on the object. We expect that this instability will be pushed to even higher loads in suckers constructed with higher spring stiffness, but have not yet investigated this possibility. We expect such a change in spring stiffness to also change the dynamics of the sucker operation at all levels and not just its load-bearing capacity.

Simulations with this larger sucker design run with parameters adjusted to the bulk modulus and the density of air as the fluid medium demonstrated that operation of such a sucker in air is feasible. Simulations with model suckers using parameters for electro-active polymer force generation replacing octopus muscle and rubber replacing collagen also demonstrated the ability to translate these principles into operating suckers of larger size than octopus suckers and in air. The strongest lift was supplied by the artificial muscles operating in air with a value of 8.2 kg. This is close to the weight that would be supported in the ideal, and unattainable, condition of perfect vacuum within the lumen against 1 atmosphere ambient pressure.

These larger suckers, however, were not able to hold these loads in place indefinitely. In general, they suffered from a dynamic instability that resulted from the lifting process itself. The upward pull of the object was vigorous and rapid, imparting considerable momentum to the object. Thus when the object was lifted upward it collided with the muscular hydrostat units above and transmitted a wave of collisions up the chain of muscular hydrostat units that terminated at the rigidly fix arm. The reflection of this wave back from the arm surface toward the object produced motions in the individual muscular hydrostat units that deformed the sucker and caused the loss of the seal and the adhesive force. So, while these larger suckers were able to lift larger loads, the duration of that hold was less than 1 s. This is a result of the rigid anchor nodes we used to hold the model sucker. In the real octopus arm or robot this instability might happen if the arm were held rigidly in place and were in a stiffened state. In a natural situation the soft octopus (or robot) arm would absorb some of energy of this wave and reflect only a small portion back. In future, more realistic, simulations with ABSAMS the use of more realistic anchor points with the ability to absorb energy will certainly resolve this difficulty.

4. Discussion

Sucker attachment systems are available commercially and have found broad application in a variety of industries. These

technologies suffer from two limitations. First, their adhesive force depends on the availability of a vacuum generator to produce and maintain useful attachment. This means that they are noisy and not very portable both of which can be undesirable in some applications. Second, the surface is a cup of fixed shape. This means that attachment quality for a variety of surfaces requires changing to a cup that matches the surface geometry. The octopus sucker system is an existence proof that a single solution is possible to both these problems. The studies reported here are aimed at the development of octopus-inspired suckers that utilize local pressure generation in a compact system and have a conformable rim that adapts to the surface dynamically. The steps toward these goals and the capabilities are made clearer by the results of our simulations.

First, though it is possible to make suckers larger than octopus suckers, and it is true that the attachment force will increase with the size of the sucker, the limits of the attachment strength of artificial suckers are determined by the fluid medium in which they operate. In water the limit is the cavitation pressure of water that is approximately 2 atmospheres (Smith 1996). This is a considerable adhesion force that accounts for the strength of the octopus's grasp. One of the contributions of these studies is to demonstrate the feasibility of translating the principles of octopus sucker design to in-air operation. In air the ideal highest pressure attainable is about 1 atmosphere (at sea level), which is the pressure difference between atmospheric pressure and a pure vacuum. For a closed volume design following the octopus sucker it is impossible to achieve a vacuum in the lumen. This places the theoretical limit of about 9 kg on suckers about 20 cm in diameter. This means, for example, that single closed-design suckers cannot attach to and hold automobiles against the force of gravity. The gains in attachment strength with increased sucker size approach asymptote above this size so it appears that single in-air octopus-inspired artificial suckers will find utility mostly in reversibly lifting and moving relatively small objects. This limitation can be overcome, as the octopus and commercial vacuum driven suckers do, by employing arrays of suckers to the extent that the geometry of the sucker delivery device permits.

Second, although the modular approach of using many muscular hydrostat units brings unique benefits of the octopus design it poses two important limitations on what we can learn from the simulation. Firstly, the muscular hydrostat concept depends on the bulk modulus of the fluid and tissue contained within the muscular hydrostat unit. For our simulations, this is such a hard constraint that we must simulate at a time step of 1×10^{-9} s in order to keep the shape changes smooth (to avoid numerical instability). Simulation time steps larger than these cause the units to 'ring' and induce destabilizing oscillations throughout the interconnected muscular hydrostat units that would never occur in real physical systems. Although this permits the exploration of realistic dynamics in muscular hydrostat unit systems, it makes the actual run time of simulations impractically slow and limits the number of elements that can be used in such simulations. Secondly, the instability of the larger suckers used in the simulations that resulted under load was partially a consequence of the

unrealistic rigidity of the muscular hydrostat unit models we used. Although our muscular hydrostat units retain their shape as they resize and collide, real soft muscular hydrostat units will deform under the action of local pressure. Including deformable muscular hydrostat units would also increase the computational load and dramatically increase simulation duration. Both of these limitations point to advantages to be had from studying muscular hydrostat units implemented in robots rather than simulations. Studies of isolated biological muscular hydrostat units (in Sherington's sense of motor units (Kandel *et al* 1991, p 15)) also present substantial technical challenges that might be clarified, and hopefully simplified, by studies with artificial muscular hydrostat units.

Vidyanathan et al (2000) implemented a muscular hydrostat robot that was capable of inch-worm locomotion. The effectors used in this robot were bags of fluid that were reshaped by externally placed shape-memory-alloy contractile elements. A similar effort that parallels the ABSAMS simulations can be imagined using muscular hydrostat units with their contractile elements located inside. They could be connected, as in the simulations reported here, into assemblies held together with connective rubber or other suitable materials to match the geometry of the sucker. Electro-magnets attached to the interior of the muscular hydrostat unit could be used to produce contractions along fixed dimensions that would result in controlled shape changes. Graded control of electromagnetic force would permit graded geometry change of the individual muscular hydrostat unit and through a network of connective elements the entire robot. Such implementations when studied would provide the physics 'for free' and avoid the numerical simulation issues that limit our use of the simulations above. The domain of muscular hydrostat unit systems is one of those research areas in which simulation cannot completely replace robot implementation in terms of lessons learned about the basic control principles. The high degrees of freedom and large numbers of interacting parts make it difficult, if not impossible, to decide a priori which physical assumptions are essential for accurate simulation.

However, important progress in the short term can be made in the direction of control systems within the simulations. The control of the suckers employed here was admittedly simple. We suspect it leads to the difficulties in holding larger objects with larger suckers by accelerating the grasped objects too quickly. The all-or-none control we used with the larger suckers produced larger forces than were necessary. These in turn accelerated the mass to be moved much faster than was necessary with the consequence that the kinetic energy of the system was forced to rapid dissipation through the structure of the sucker. The use of sub-sub maximal muscle activation and careful timing of the sequence of muscular hydrostat unit activation offer the resolution of practical issues for suckers, robots and general control of multi-muscular hydrostat unit systems. Regardless of the implementation of multi-muscular hydrostat unit systems in robots to deal with the computational realities of simulation, the study of these control issues will yield important insights into problems of hyper-redundant control already solved by the octopus.

The neural control of octopus suckers in particular and cephalopod muscular hydrostats in general, has been the

subject of a small amount of research. It is not known whether graded or all or none control is employed at the level of biological muscular hydrostat units. Evidence for parallel channels of all-or-none and graded response has been found for squid mantle muscle (Gilly et al 1996) but similar studies of sucker control have not been undertaken. The role of the nerve roots in controlling the motions of the isolated octopus arm has recently been studied (Gutfreund et al 2006). The patterns of activation found there agree with the motor unit concept in that the whole muscular hydrostat is not activated by electrical stimulation of the nerve but only local regions. Overall, however, the study of the neural mechanisms of control in muscular hydrostat systems is a fundamental area of basic research that will provide new control mechanisms. Given the difficulties of studying muscular hydrostats and muscular hydrostat units in situ it is not surprising that simulation studies have proven important in providing insights in the mechanisms by which actuation is realized and control is exerted (Gutfreund et al 1996, 1998, 2006, Sumbre et al 2001, 2006, Walker et al 2006, Liang et al 2006). Until some major methodological advance that permits direct study of individual muscular hydrostats and muscular hydrostat units in situ (and in isolation) becomes available it is likely that simulation will continue to play a key role in developing our understanding of their control and coordination.

The remarkable flexibility of octopus arms, elephant trunks and other biological muscular hydrostat systems has generated considerable excitement as a source of inspiration for continuum robotics and new technologies. As a result many previous models of muscular hydrostat systems have aimed at capturing the flexibility of muscular hydrostats; their ability to form an arbitrary number of 'joints' at arbitrary locations and that bend in arbitrary directions. Our simulation approach emphasized the impact of local control, non-homogenous muscular hydrostat components and non-isotropic arrangements of connective tissue on muscular hydrostat system functions that are constrained in direction rather than arbitrary. The octopus sucker was a natural biological structure to model for this purpose: in it several muscular hydrostats, of different sizes and spatial arrangements that act in temporal coordination to provide directed actuation on objects in the world. Our simulation led us to several insights about how this directed coordination is achieved. Observations of the role of the model sucker sphincter played in dynamically stabilizing the interaction of the acetabulum and infundibulum during the adhesion cycle is important in providing an indication of the kinds of structural specializations that may be required of muscular hydrostat systems to permit them to make controlled contact with physical surfaces. As the study of biological muscular hydrostats and their function matures we are likely to find more examples of these task-specific adaptations of muscular hydrostats in biology and with them new schemes for the control and coordination of actuation and behavior.

Acknowledgments

The research reported here was supported by the DARPA DSO BioDynotics Program (subcontract 882-7558-203-2004599 to FG) program officer: Morley Stone. This paper was presented at the 2006 International Symposium for Biologically Inspired Design in Science and Engineering sponsored by the Center for Biologically-Inspired Design at Georgia Tech, Atlanta Georgia and we thank the organizers, Jeannette Yen and Marc Weissburg for their invitation to participate. Jun Wu and Apoorva Kapadia of the BCR lab contributed technical assistance with the C++ programming and simulations. We thank Bill Kier and Andrew Smith for their generous and helpful discussions of the principles by which octopus suckers and muscular hydrostats work. We thank Jennifer Basil of Brooklyn College for helpful comments on and proofreading of the manuscript. We also thank two anonymous reviewers and Marc Weissburg for thoughtful constructive comments on the manuscript.

References

- Faulkner W R P D, King J W M P and Damm H C P 1968 Handbook of Clinical Laboratory Data 2nd edn (Cleveland, OH: Chemical Rubber Co.)
- Fiorito G, Von Planta C and Scotto P 1990 Problem solving ability in Octopus vulgaris Lamark (Mollusca, Cephalopoda) Behav. Neural Biol. 53 217–30
- Gilly W F, Preuss T and Mcfarland M B 1996 All-or-none contraction and sodium channels in a subset of circular muscle fibers of squid mantle *Biol. Bull.* **191** 337–40
- Gutfreund Y, Flash T, Fiorito G and Hochner B 1998 Patterns of arm muscle activation involved in octopus reaching movements *J. Neurosci.* **18** 5976–87
- Gutfreund Y, Flash T, Yarom Y, Fiorito G, Segev I and Hochner B 1996 Organization of octopus arm movements: a model system for studying the control of flexible arms *J. Neurosci.* 16 7297–307
- Gutfreund Y, Matzner H, Flash T and Hochner B 2006 Patterns of motor activity in the isolated nerve cord of the octopus arm *Biol. Bull.* **211** 212–22
- Hanlon R T and Messenger J B 1996 *Cephalopod Behaviour* (Cambridge: Cambridge University Press)
- Hannan M A and Walker I D 2003 Kinematics and the implementation of an elephant's trunk manipulator and other continuum style robots J. Robot. Syst. 20 45–63
- Kandel E R, Schwartz J H and Jessell T M 1991 Principles of Neural Science 4th edn (New York: McGraw-Hill—Health Professions Division)
- Kier W M 1988 The arrangement and function of molluscan muscle Mollusca 11 211–52
- Kier W M and Curtin N A 2002 Fast muscle in squid (Loligo pealei): contractile properties of a specialized muscle fiber type *J. Exp. Biol.* **205** 1907–16
- Kier W M and Smith K K 1985 Tongues, tentacles and trunks: the biomechanics of movement in muscular-hydrostats Zool. J. Linnaean Soc. 83 307–24
- Kier W M and Smith A M 1990 The morphology and mechanics of octopus suckers *Biol. Bull.* 178 126–36
- Kier W M and Smith A M 2002 Symposium on the Biomechanics of Adhesion (Anaheim, CA: Society for Integrative and Comparative Biology) pp 1–24
- Kier W M and Van Leeuwen J L 1997 A kinematic analysis of tentacle extension in the squid *Loligo Pealei J. Exp. Biol.* 200 41–53
- Laszlo M J 1996 Computational Geometry and Computer Graphics in C++ (Englewood Cliffs, NJ: Prentice-Hall)
- Liang Y, McMeeking R M and Evans A G 2006 A finite element simulation scheme for biological muscular hydrostats J. Theor. Biol. 242 142–50

- Mather J A 1994 'Home' choice and modification by juvenile Octopus vulgaris (Mollusca: Cephalopoda): specialized intelligence and tool use? *J. Zool.*233 359–68
- O'Rourke J 2005 *Computational Geometry in C* (Cambridge: Cambridge University Press)
- Robinson G and Davies J B C 1999 Continuum robots—a state of the art *Robot. Autom.* **4** 2849–54
- Shreiner D 2000 *OpenGL Reference Manual* (Indianapolis: Pearson Education)
- Smith A M 1991 Negative pressure generated by octopus suckers: a study of the tensile strength of water in nature *J. Exp. Biol.* **157** 257–71
- Smith A M 1996 Cephalopod sucker design and the physical limits to negative pressure *J. Exp. Biol.* **199** 949–58
- Sumbre G, Fiorito G, Flash T and Hochner B 2006 Octopuses use a human-like strategy to control precise point-to-point arm movements *Curr. Biol.* **16** 767–72
- Sumbre G, Gutfreund Y, Fiorito G, Flash T and Hochner B 2001 Control of octopus arm extension by a peripheral motor program *Science* **293** 1845–8

- Van Den Bergen G 2004 *Collision Detection in Interactive 3D Environments* (San Francisco: Morgan Kaufmann)
- Van Leeuwen J L and Kier W M 1997 Functional design of tentacles in squid: linking sarcomere ultrastructure to gross morphological dynamics *Phil. Trans. R. Soc. Lond.* 551–71
- Vidyanathan R, Chiel H J and Quinn R D 2000 A hydrostatic robot for marine applications *Robot. Auton. Syst.* **30** 103–13
- Voight J R 1993 The arrangement of suckers on octopodid arms as a continuous character *Malacologia* **35** 351–9
- Walker I D 2000 Proc. Int. Symp. on Adaptive Motion of Animals and Machines (Montreal, Canada)
- Walker I D, Dawson D M, Flash T, Grasso F W, Hanlon R T, Hochner B, Kier W M, Pagano C C, Rahn C D and Zhang Q M 2006 Proc. 2005 SPIE Conf. on Unmanned Ground Vehicle Technology VII (Orlando, FL) vol 5804, pp 303–14
- Weast R C 1976 Handbook of Chemistry and Physics (Boca Raton, FL: CRC Press)
- Yekutieli Y, Sagiv-Zohar R, Aharanov R, Engle R, Hochner B and Flash T 2005 Dynamic model of the octopus arm.
 I: Biomechanics of the octopus reaching movement *J. Neurophysiol.* 94 1443–58