Reverse Engineering the Octopus Arm

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Abstract

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Despite the extreme flexibility of the octopus's arms and their resulting near infinite possible configurations, the octopus effectively controls its arms for use in a wide range of behaviors, including locomotion, foraging, excavation, exploration, and manipulation. These behaviors also gain a number of advantages from this extreme mechanical flexibility. The octopus not only successfully controls limbs with infinite degrees of freedom, but prevalently exploits this biomechanical property to generate adaptive behavior. The octopus therefore serves as an ideal model for soft robotics. If appropriately characterized, the octopus's biomechanical properties and control strategies could be implemented in the development of a soft robotic limb with the same range of capabilities.

Many of the octopus's behaviors, such as when foraging at night or in visually occluded spaces, are executed under conditions of limited or absent visual feedback. In such conditions,

the octopus must rely primarily on the complex chemotactile system of its suckers to successfully find and capture prey. The investigations presented here aimed to characterize the search strategies used by the octopus in such conditions and identify the primary control mechanisms driving these strategies. Sucker recruitment was revealed to be a key mechanism employed during search, and one that can be adapted to perform systematic search patterns over complex surfaces. This mechanism also provides a number of other behavioral and computational advantages to the octopus, which are discussed, and was therefore implemented in the development of a soft robotic arm. Inspired by the repeated sucker units of the octopus arm, this robotic arm was created by designing the mechanical properties and control algorithm of a single segment, then simply replicating this segment and assembling the replicates end-to-end.

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Chapter 1. Introduction

Like other cephalopods, the octopus shared a common ancestor with vertebrates over 500 million years ago. Since the existence of this simple bilaterian ancestor, the cephalopods emerged as the most complex invertebrate in virtually every level of their biological organization, and this complexity evolved along an evolutionary path separate from that of vertebrates. This parallel evolution of complexity, particularly in behavior and cognition, poses the cephalopods as an alternative model for intelligence. Such a model can help us understand the diversity of forms intelligence might take as it evolves on other worlds, and serve as biological inspiration for the development of behaviorally flexible robotics.

Despite in many respects demonstrating cognitive complexity rivaling that of vertebrates, the octopus's body plan and nervous system is organized unlike anything seen among vertebrates. Most of the octopus's nervous system is distributed within its arms and suckers (Young, 1971). Without a skeleton, the octopus's eight arms are incredibly flexible and capable of adopting any one of an infinite range of possible configurations. Each arm bears hundreds of suckers used to interact with the environment during a wide range of behaviors. Each of these suckers bears a densely organized sensory field of mechanical and chemical receptors both numbering in the tens of thousands (Graziadei, 1965a) (for comparison, the human fingertip bears a few hundred mechanical receptors). The octopus is therefore able to gather massive amounts of sensory information from the environment at once, but most of this information is not communicated to the brain. A very small bandwidth of neural pathways connects the arms and brain (Young, 1965; Matzner et al., 2000; Rokni & Hochner, 2002; Nesher et al., 2019), and among the information not represented by these pathways is proprioception reflecting the shape of the arms and suckers (Wells & Wells, 1957; Wells, 1964; Rowell, 1966). Without this information, the brain is limited in its ability to send a detailed motor plan to the arms. Instead, the brain will send out a broad, generalized motor plan which activates motor pathways localized within the arms and suckers (Zullo et al., 2009; Zullo et al., 2019). These pathways then integrate the mechanical and chemical information from the suckers to adapt behavior to the immediate mechanical and chemical makeup of the environment. These unique features of the octopus's control system and their significance to robotics are discussed in Chapter 2.

Without visual feedback, the octopus must rely primarily on the chemotactile system in its suckers to navigate tasks, and any indication of arm shape provided by visual cues is removed. Chapters 3 and 4 investigate searching behavior in visually occluded spaces and identify sucker recruitment, a mechanism localized within the arms, as playing a prominent role in these conditions. When a sucker encounters a stimulus, the neighboring suckers will bend toward this stimulus, which may likewise recruit their neighbors in the same way (Rowell, 1963; Altman, 1968; Gutfreund et al., 2006; Zullo et al., 2011). This causes the arm to conform to the shape of surfaces in the environment, and by doing this, the octopus has effectively delegated the decision of arm shape to the arms themselves and the mechanical and chemical makeup of the environment as it is conveyed by the suckers. This mechanism serves to limit the degrees of freedom of the octopus arm. Rather than the octopus choosing one of an infinite number of muscle adjustments to reshape its arm, the surface acts as a guide, shaping the arm with a local sensory-motor feedback mechanism. The octopus therefore uses surfaces much like how a ship may use coastlines for navigation. Comparatively, when reshaping its body a vertebrate or arthropod does so at a limited number of joint locations. Surface features therefore appear to play an analogous role for the octopus as our skeleton does for us: our brain commands our arm to bend and our skeleton determines where. Meanwhile, the octopus brain commands its arm to bend and the environment determines where. Beyond its operational and computational significance, recruitment contributes to prey capture, grabbing and manipulating objects of any shape, evaluating the salience of sensory input, and performing a systematic search pattern over complex surfaces.

These motor pathways like the kind driving recruitment and their corresponding behaviors operate with minimal feedback from the brain and many remain intact when the arm's connection to the brain is severed (Rowell, 1963; Graziadei, 1965b; Rowell, 1966; Altman, 1968; Sumbre et al., 2001; Gutfreund et al., 2006; Zullo et al., 2011; Hague et al., 2013; Katz et al., 2021). The extent to which the octopus relies on decentralized computation to adapt its behavior to the environment stands in sharp contrast to us and other primates, who are unique among animals in the direct connection between our motor cortex and motor neurons (Pearson & Gordon, 2013)), giving us direct and detailed command over our movement, and the ability to encode it into memory. Behavioral flexibility can therefore be attributed to different levels of biological organization in primates and octopus. Primates have very limited degrees of freedom inherent to their movement, allowing for information about the body's configuration during movement to be stored within the brain. Behaviors may therefore be adapted and improved through trial and error. Meanwhile, the octopus can fit through confined, convoluted spaces over a wide range of sizes and shapes, grab and manipulate objects of any shape, and maneuver over uneven terrain. However, the mechanical flexibility that generates this behavioral flexibility means that the octopus cannot encode the details of movement into memory.

The organization of the octopus's nervous system, while supporting a great deal of behavioral and mechanical flexibility, places many limitations on the octopus's ability to learn skilled movements (Wells, 1961). Consequentially, many of the defining features of the octopus's intelligence prohibit the kind of motor control needed for the development and use of tools and technology. While there is of course no knowing for sure what future cephalopod evolution will make of the current body plan, the octopus's evolutionary trajectory so far has generated an intelligence wholly unlike the technological intelligence of humanity, and lacks a number of the key neural and morphological characteristics that preceded the dawn of technology for our ancestors. The significance of the octopus as a model for extraterrestrial intelligence is therefore likely not in representing what we would find at the far end of a radio signal or aboard an interstellar spacecraft. Instead, the octopus's unique combination of computationally complex adaptations perhaps represent a variety of intelligence that we will specifically not find with such technological capabilities. Ultimately, this helps to narrow down the varieties of intelligence whose traces we will find in our search for life in the universe.

As a model for artificial intelligence, the octopus takes on a different and more immediate relevance. Advances in computing technology have shown dramatic leaps in decentralization, and the vast and rapidly growing network of autonomous users, data, processors and machine learning algorithms that comprises the internet has created forms of intelligence for which there are few analogs in the biological world. On the other hand, as a computationally and morphologically complex limb used in a wide range of behavior, the octopus arm serves as a promising biological basis for the development of soft robotics with a great number of applications.

Over billions of years of evolution, life has generated an endless source of inspiration for paradigm-shifting technology and robotics in particular has massively benefited from the mechanical and computational properties of living organisms. The emerging field of soft robotics is an especially promising avenue to explore the varieties of morphological properties and control strategies employed in the biological world. As potential alternatives to traditionally rigid robots used for planetary exploration, soft robots are lightweight, low-volume, and flexible. With the octopus arm able to fit through and explore confined spaces, grasp and manipulate objects of any shape, maneuver over uneven terrain, and operate autonomously with little feedback from a centralized controller, implementing the biomechanical and computational properties of the octopus arm in the development of soft robotics could further our exploration into the most hostile environments on Earth and beyond.

In a number of the octopus's most common behaviors, no particular sucker or length of arm is functionally vital or unique. Therefore, what seems to be a useful approach to controlling limbs with infinite possible configurations is to perfect a single unit mechanically and computationally and assemble multiple units end-to-end. In Chapter 5, I adopted this approach for the design and development of a pneumatically controlled soft robotic arm. The prevalence of recruitment as a control strategy and in its key role in a number of behaviors posed it as a useful initial behavior to implement within this robotic arm. If properly implemented, this behavior could provide the same functional and computational benefit for the robot as it does for the octopus. To ensure precise and abundant replicates, I designed the components of an arm segment and 3D printed them. Each segment included four soft actuators and a gripper that likewise served as a contact sensor. Each segment was programmed to bend toward its neighbor in response to activation of the neighboring gripper, which served as a simple implementation of sucker recruitment in robotic form. The soft components of this limb were printed using a novel approach: by printing only the outer shell of a 3D object in one spiraled extrusion (a printer setting known as "vase mode") using a soft thermoplastic polyurethane filament. With consideration given to the surface gradient in designing the object shape and to the relevant printer settings, vase mode in combination with a flexible filament can print soft, tight sealing bladders in a wide variety of shapes. This also made for very light components overall and conserved material compared to alternative printing methods.

In addition to creating a limb that could foreseeably have the full range of behaviors as the octopus arm, this fabrication method presents a number of advantages. Segments can be easily resized and alternative materials can be used depending on the application and environmental conditions. Segments can be manufactured with minimal human involvement, and the design can be improved to be able to print a fully functional limb with one print, effectively removing the need for human assembly. Pneumatic control can be replaced with hydraulic control for use in liquid. Finally, cheaper and more widely available materials, software, electronics, control hardware, and 3D printers may be used as alternatives to what was used here, which would allow for a greater number of people to benefit from this technology and contribute to its development.

In the context of planetary exploration, an approach like the one used here could lead to a future of light-weight, versatile soft robot explorers with the capacity to traverse complex terrain types, explore through confined, convoluted spaces, and manipulate a vast range of objects. The lava tubes of Mars and plume vents of Enceladus are sites that could particularly benefit from this kind of robotic explorer. With a segmented design and 3D printed manufacturing, robot components could be easily replaced or extended, and this could be done with recycled material from damaged components.

If we wish to create robots with the behavioral range of biological organisms, we need to learn by example. In the biological world, the use of rigid materials is very limited. Much of the adaptivity, robustness, and resilience we see in nature can be largely attributed to soft materials (Pfeifer et al., 2014). Even skeletons (which in humans accounts for less than 15% of body weight (Gropper & Smith, 2012)) are actuated by muscle and held together by tendons, ligaments, or membranes. It is crucial, therefore, that we embrace the use of soft materials in the development of robotics, and planetary explorers are no exception.

With the goal of using the octopus's control strategies to develop a control framework for soft robotics, in the following chapters I review the architecture of the octopus's nervous system and the mechanisms used to control its arms (Chapter 2), investigate the role of one of these mechanisms (sucker recruitment) in search behavior without visual feedback (Chapter 3) and how this mechanism can be adapted to perform systematic search patterns over complex surfaces (Chapter 4). Finally, I implement this mechanism in the development of a soft robotic arm (Chapter 5).

Chapter 2. Lessons for robotics from the control architecture of the octopus

2.1 Introduction

The octopus's movement is not limited by joints or a rigid skeleton. With the ability to bend its eight arms in any direction at any point along their length, the octopus's space of possible configurations vastly exceeds that of skeletal animals such as vertebrates or arthropods.

The octopus brain outsources much of the circuitry necessary to control its arms into the arms themselves, where a network of ganglia coordinates sucker and arm behavior with limited feedback from the brain (Young, 1971).

Scientific interest in the octopus has found an application in the development of flexible, adaptable robots (Walker et al., 2005; Calisti et al., 2011; Margheri et al., 2012; Walker, 2013; Nesher et al., 2014; Krieg et al., 2015; Nakajima et al., 2017; Mazzolai et al., 2019). Like the octopus arm, the movement of such robots is hyper-redundant—the high number of degrees of freedom for the robot vastly exceeds those necessary to accomplish most tasks (Walker et al., 2005; Trivedi et al., 2008).

With its ability to combine extreme flexibility with precise manipulation and locomotion, the octopus represents an effective solution for the significant control problems facing soft robotics (Walker et al., 2005; Calisti et al., 2011; Levy et al., 2019). Much of the modern work in octopus motor control has been focused on understanding how the octopus controls its arms despite their vast configuration space, and how this can be applied in the development of soft robotic controllers (Walker et al., 2005; Calisti et al., 2011; Nesher et al., 2014; Mazzolai et al., 2019).

Here we will describe the neuroanatomical organization of the octopus peripheral nervous system and discuss how this distributed neural network is specialized for effectively mediating decisions made by the central brain and the control of limbs possessing an extremely large number of degrees of freedom. We will describe the hierarchical organization of information in this system (Wells, 1978; Zullo et al., 2009), and propose three neuromechanical mechanisms within this organization that reduce the computation necessary for generation of the octopus's arm behavior: 1) Hierarchical hybrid action selection, which allows for simple motor commands from the brain to be integrated with sensory information from the arms, 2) ascending recruitment, a mechanism of multi-sucker and multi-arm coordination which serves as a strategy for novelty-detection and as an adaptive filter for mechanosensory input, and 3) contact-based navigation and manipulation, which, along with other sensory cues, constrain the degrees of freedom of the octopus's limbs to a limited range of configurations. We will likewise discuss how these mechanisms can serve as control strategies in soft-robotics.

2.2 Existing Approaches in Robotics

2.2.1 Robotics Terminology

Typical rigid robots are described in terms of rigid links connected by joints, which allow motion. Rotary joints, for example, allow the angle between links to change, while prismatic joints allow the length of a link to change. If a robot has N joints, then the pose (or configuration) of the robot can be described using a vector of N values, each representing one of the robot's joint values. The task space or the work space of the robot is the three dimensional space in which it operates. The configuration space is an N-dimensional mathematical space whose axes represent the potential values of the robot's joint angles. Each pose of the robot can be represented as a single point in this space. A robot's trajectory through time can be represented as the motion of this point through the configuration space. Kinematics refers to computing the position and orientation of all the robot's joint angles; inverse kinematics means computing the joint angles necessary to bring the robot's end effector (for example) to a particular position and orientation (or pose) in the workspace. Obstacles that have a simple geometry in task space, such as a flat table surface or a wall, lead to constraints in configuration space with very complex geometries. The high dimensionality of configuration space, together with the complex geometry of constraints in configuration space, makes robotic planning (the selection of sequences of actions) a difficult computational problem. For an octopus with a very large number of degrees of freedom, the conventional robotics approach to planning and control appears to be computationally intractable. The process of modeling and predicting motion at higher velocities where inertia must be considered is referred to as dynamics in the robotics literature. The computational challenges posed by the octopus are great even using a simplified kinematic framework that ignores dynamics; the computational problems that arise when dynamics is considered become even more challenging.

2.2.2 How Many Degrees of Freedom Does an Octopus Arm Have?

It is usual to categorize a rigid robot arm by the number of joints or degrees of freedom, or using the terminology above, the dimensionality of its configuration space. Therefore it is natural for roboticists to wonder about the configuration space of an octopus arm: how many dimensions is it? How many degrees of freedom does an octopus arm have? We suggest that the question must be refined. We will propose to discuss the octopus arm in terms of several types of degrees of freedom. The octopus arm is highly compliant: it can be deformed simultaneously at a vast number of independent locations. Thus we might say that it has a very large number of passive degrees of freedom. These are not actuated or directly controllable; rather, when the arm presses against a rigid object, the passive degrees of freedom allow the arm to conform to that object at a large number of points. At another extreme, the octopus exhibits certain arm-scale behaviors that are analogous to robot arms: it bends at a small number of pseudo-joints, which are analogous to rotary joints in a robot arm; and sections of the arm can elongate or shorten, which could be modeled as a small number of prismatic joints. Thus the arm could potentially be characterized by a relatively small number of global arm state degrees of freedom, which would be analogous to the configuration space of a conventional rigid robot arm (One significant difference, however, is that the octopus can change the number of rotary joints dynamically). The octopus arm is also capable of mechanical impedance modulation: adjusting its stiffness above and below a bend. And it can control torsion, rotating around the arm's axis.

The octopus also has a large number of locally controlled degrees of freedom. Each sucker is controlled by local neural circuitry within the arms. In addition to controlling the sucker pose, this circuitry also innervates and activates the surrounding arm musculature (Gutfreund et al., 2006), which generates the forces and shape of the arm (Kier and Smith, 1985).

We believe that the large number of locally controlled degrees of freedom is a key feature of the octopus that is not present in today's robots; the primary inspiration for robots we propose to take from the octopus is the use of locally controlled degrees of freedom to simplify planning and control for the arm.

Like the octopus, today's soft robots have a large number of passive degrees of freedom. Thus this feature of the octopus is known in parts of robotics (specifically, in soft robotics). There are also many rigid robots which use long range visual sensing followed by planning to generate reaching and grasping behaviors in an arm with a small number (often seven or less) of active degrees of freedom. The problem of using long range visual sensing to plan for a small number of active degrees of freedom is computationally tractable; the problem of using vision and planning to control a large number of active degrees of freedom is much harder (apparently intractable) computationally. Controlling a large number of degrees of freedom becomes computationally tractable by making them passive and using contact-based interaction to control them. Thus the octopus's centrally planned behaviors also are similar to known techniques in robotics. The feature of the octopus that differentiates it most clearly from today's robots is the use of a large number of locally controlled degrees of freedom. Challenges for robotics include the mechanics and sensing required to build such systems, as well as understanding their function at an algorithmic level.

2.2.3 Task Domains in Robotics

Robotics can be divided into task domains and capabilities which are necessary to perform these tasks. Grasping typically means using a robot hand or gripper to immobilize an object relative to the robot arm, so that the robot can move the object. Manipulation is a more general term that indicates any robot-induced change to the state of one or more objects. The sequence of operations of grasping, lifting, moving, and setting down are examples of a manipulation procedure. In-hand manipulation means changing the pose or state of an object (for example by rotating it) without setting it down. Manipulation operations often involve multiple objects, such as inserting a peg in a hole or a key in a lock.

The task domain of navigation and locomotion encompasses moving within an environment. For example, a wheeled robot might navigate using the following capabilities: sensing the environment with lidar to determine the locations of obstacles, the perceptual process of building a map of the environment, planning a route on the map that brings the robot to the target location without collision, and executing the plan. Executing the plan involves actuation, the generation of the locomotive force using electric motors, and low level feedback control to overcome errors such as wheel slippage.

The field of soft robotics aims to create robots with mechanical properties and actuation capabilities that are similar to the octopus, in particular compliance. This paper does not focus on actuation per se; this topic is covered thoroughly in reviews on soft robotics (Kim et al., 2013; Galloway et al., 2016; Manti et al., 2016; Polygerinos et al., 2017; Cianchetti et al., 2018; Whitesides, 2018). The paper also does not focus on sensing; since the technological substrates are so different, it is difficult to extract inspiration for today's engineered systems from octopus sensing. Instead, the paper focuses on the computational level: planning and control, where we believe that system-level inspiration can be most readily extracted today.

2.2.4 Behavioral Architectures for Robotic Systems

The most widely accepted architecture for robotic systems is known as "sense, plan, act" (Nilsson, 1982). In this paradigm, sensors transduce physical signals, perceptual processes build models of the physical world, planning processes search through the space of potential actions to generate sequences expected to lead to favorable outcomes, and then the best sequence of actions is executed. In the "purest" form of sense-plan-act, the entire plan would be executed "open loop," in other words without further sensing or control. The main disadvantages of an open loop approach are that the perceptual and planning processes are computationally demanding and brittle or error prone. A closed loop control process is able to compensate for sensing or actuation errors, ideally overcoming perturbations to restore the robot's state to the planned trajectory.

Proposed alternatives to the sense-plan-act approach include the more biologically inspired subsumption architecture (or reactive or behavior-based robotics) (Brooks, 1986; Payton, 1986; Agre and Chapman, 1987; Firby, 1987; Brooks, 1990). This approach couples sensors more directly to actuators in tight control loops while higher level computational processes modulate and compose these lower level behaviors. Advantages of this approach include fast and dynamic robot behavior, the ability to respond to dynamically changing environments, lower computational requirements, and insensitivity to modeling errors, since the robot does not construct an explicit model of the environment. In the purest form of this approach, the environment functions as its own representation; rather than the robot considering its own internal computational model of the environment, the robot would consult its own sensors to collect required information about the state of the world at the present moment. Disadvantages of this approach are that the behaviors tend to be "greedy," and thus less intelligent than approaches that are able to avoid local minima. Greedy is a term used in computer science to describe an algorithm in which, at each time step, the action is selected that provides the greatest reward in that time step. Explicit planning approaches are able to delay gratification, selecting actions in the present with lower immediate rewards, but with higher rewards predicted later. For example, consider a simple robotic scenario in which a robot, which knows its position, is attempting to navigate to a goal by following a map. Faced with a branch in the road, the greedy approach is to always select the road that (at the particular location where the choice must be made) heads most closely in the direction of the goal. However, without the capability to look ahead on the map, this can lead to the robot becoming stuck in a dead end. A smarter, non-greedy approach would consider the future benefits of choosing a particular sequence of road choices. This can allow the robot to avoid getting stuck in dead ends.

Low level fast reactive control has been explored for integration with robot manipulators in proximity perception (Mayton et al., 20102010; Navarro et al., 2021) as well as visual servoing (Espiau et al., 1992).

Recently Model Predictive Control (MPC) has seen a resurgence in robotics. MPC is a version of the sense-plan-act approach but modified to be more reactive and dynamic. In MPC, the sensing and planning steps occur as usual, but only the first step of the action plan is executed. Then the sense-plan-act cycle starts again. The frequent sensing and re-planning allow the robot to react dynamically to changes in the environment, while still making more intelligent choices than a purely reactive system (Erez et al., 2011; Lenz et al., 2015; Zhang et al., 2016; Liu et al., 2017; Williams et al., 2017; Gillespie et al., 2018; Amos et al., 2019; Kabzan et al., 2019). In terms of computational resources, it requires even more than the conventional sense-plan-act cycle, since plans are being constantly generated and re-generated. We will discuss how the control architecture of the octopus may provide benefits reminiscent of MPC but with lower computational costs.

2.2.5 Underactuated Robotics

Underactuated robotics (Spong et al., 1998; Reyhanoglu et al., 1999; Birglen et al., 2008) makes use of systems in which the number of individually controllable degrees of freedom is less than the number of degrees of freedom of the mechanism. For example, robot hands have been designed with just one actuated degree of freedom (one motor), but multiple joints (Odhner et al., 2014; Deimel and Brock, 2016). When the robot contacts an object to be grasped, it conforms to the object's shape. We will discuss ways that the octopus uses an analogous strategy.

2.2.6 Contact-Rich Dynamics

It is typical in robotics to sense and plan in order for the robot to avoid collisions with obstacles or objects. There are some exceptions which explicitly consider planning and control through contact. In manipulation, contact is necessary, but is avoided as long as possible, and the planning process tends to focus on the motions before contact. Legged locomotion is another area in which contact (between the leg and the ground) must be considered, and most of the robotics work that considers contact originates from legged locomotion (Erez et al., 2011; Posa et al., 2014; Marcucci et al., 2017; Pace and Burden, 2017; Deits et al., 2019).

2.2.7 Planning on Constraint Manifolds

Even simple motion constraints, such as a planar table top or wall, produce complex geometries in the configuration space of a robot arm with several degrees of freedom. A robot arm moving its end effector along a table top corresponds to motion within a lower dimensional sub-space of the arm's full configuration space; this subspace is known as a constraint manifold. The general problem of generating motion plans that remain within such a constraint manifold is a challenging computational problem because of the high dimensionality of the space and the complexity of the geometry (Berenson et al., 2009; Berenson et al., 2011). For an octopus to use a centralized approach to generate a motion plan that moves its arm along a complex surface would likely be computationally infeasible: the number of degrees of freedom of the octopus arm is much higher than a typical articulated robot arm and many parts of the octopus arm touch the surface simultaneously. In the next section we describe the approach that appears to be used by the octopus, and discuss the potential for robots to make use of this strategy.

2.2.8 Hybrid Control

Hybrid control refers to hierarchically organized systems that choose among discrete control modes at higher levels, and for each of these modes, different continuous controllers operate at lower levels (Branicky et al., 1998; Goebel et al., 2009). The term hybrid refers to the combination of discrete and continuous dynamics. The control strategy of the octopus shares some features with hybrid control.

2.3 Mechanical Properties of the Octopus

The octopus's arms, like elephant trunks, earthworm bodies, and vertebrate tongues, are muscular hydrostats (Kier and Smith, 1985; Kier and Stella, 2007). Unlike skeletal muscle, which relies on skeletal elements to support the generation of movement, muscular hydrostats generate force and serve as the support for movement. In the octopus arm these muscles are arranged in transverse, longitudinal and oblique (helical) orientations. The requirement of the hydrostat to maintain constant volume ensures that when the transverse muscles decrease the cross-sectional area of the arm, the arm increases in length. Likewise, as the longitudinal muscles contract and the arm shortens, the cross-sectional area increases. The interplay of the three muscle groups and the lack of inherently rigid structure equips the arm with its remarkable flexibility (Kier and Smith, 1985; Kier and Stella, 2007; Kennedy et al., 2020).

The capacity for robots to generate adaptive behavior can be facilitated by exploiting their material properties. Elasticity, for instance, can stabilize the body during motion, while compliant properties can allow an effector to adapt to the shape of an object for grasping and manipulation (Pfeifer et al., 2014). These characteristics can be both energetically and computationally favorable. As muscular hydrostats capable of complex motion over a vast range of configurations, the octopus arm serves as a particularly interesting model for the study and implementation of material properties in control architectures.

Within the arrangement of the arm's muscles are embedded arrays of collagenous connective tissue fibers (Kier and Stella, 2007; Fossati et al., 2011). The material properties of the collagen fibers give this tissue inherent stiffness, and to some degree extensibility and elasticity (Gutnick et al., 2011). In muscular hydrostats, these properties can transmit stress during motion, store elastic energy, and provide structural reinforcement (Di Clemente et al., 2021). Di Clemente et al. (2021) investigated the contribution of these properties to the arm's elasticity and stiffness and the possible roles they play in the arm's motion. The distinct formation of the fibers within the longitudinal and transverse muscles were shown to give the two muscle groups different mechanical properties. Di Clemente et al. suggest that these properties indicate a possible role of longitudinal muscles in energy storage and shock absorption, and transverse muscles in maintaining posture and resisting deformation. Overall such passive properties can locally modulate behavioral responses while minimizing their energetic cost and alleviating the computational need for neural feedback (Di Clemente et al., 2021). Not only can mechanical properties of the arm facilitate computation, some evidence points to the potential of these properties to serve a direct computational role (Nakajima et al., 2013; Nakajima et al., 2014; Nakajima et al., 2015). This potential role of both biological and artificial material properties presents fascinating directions for the field of robotics.

2.4 Architecture of the Octopus's Control System

Most of the octopus nervous system exists within its eight arms (Young, 1971). Down the center of each arm, a nerve cord (known as the arm or axial nerve cord) runs parallel to the suckers, 200–300 of which are staggered down the ventral side of the arm (Young, 1965; Gutfreund et al., 2006). The nerve cord consists of a dense, continuous network of neural circuitry (neuropil) which projects from a surrounding layer of unipolar nerve cell bodies. The neuropil enlarges at the base of each sucker. These enlargements are commonly referred to as ganglia and the sections between them as the interganglionic regions. As with other elements of the octopus's peripheral anatomy, there has been some inconsistency in the terms used for these elements. Such terms include arm ganglia (Zullo et al., 2011), axial ganglia (Rowell, 1963; Rowell, 1966), brachial ganglia (Graziadei, 1965b; Graziadei and Young, 1971; Gutfreund et al., 2006), sucker ganglia (Young, 1963; Young, 1965; Altman, 1968), and medullary cord (Zullo et al., 2019). We will refer to these elements as brachial ganglia. These ganglia serve as local sensorimotor integration centers for their corresponding suckers and nearby arm musculature, and account for about 350 million of the octopus's over 500 million neurons (Young, 1963; Rowell, 1966; Budelmann and Young, 1985). Two bundles of nerve fibers called the axonal tracts run along the nerve cord dorsal to the ganglia. At the base of the arm the axonal tracts fuse and continue to the brain as the brachial nerve, which serves as a pathway through which the ganglia communicate with the brain via the axonal tracts. The brachial ganglia are connected to their immediately distal and proximal neighbors through the neuropil (Graziadei and Young, 1971), and there is some evidence suggesting a connection through the axonal tracts (Altman, 1968). The eight brachial nerves of the arms converge on the brachial lobe of the brain. Where the brachial nerve and the nerve cord meet, the interbrachial commissure interconnects the nerve cords of the arms into a neural ring, allowing communication between arm networks independent of the brain (Altman, 1968).

Figure 2.1 shows the neural architecture of the octopus with estimated neuron and axon numbers indicated. Consistent with ganglia being sensorimotor integration centers, the vast majority of their neurons (120,000 of 130,000) seem to integrate sensory and motor information (Young, 1963; Young, 1965; Rowell, 1966). Following sensory integration in the ganglia there is a dramatic reduction in the number of sensory pathways between the suckers and the brain, with an estimated reduction from 18 million sensory neurons within the suckers to 140 thousand neurons entering the brain from the brachial nerves (Young, 1965).

Similarly, the pathways through which the brain communicates motor commands to the arms are orders of magnitude smaller than the local innervation of the musculature by the ganglia. Collectively, the brachial nerves contain an estimated 32 thousand efferent (outbound) axons, while an estimated 3 million motor neurons terminate on the musculature of the arms and suckers from the neuropil of the nerve cords (Young, 1965; Matzner et al., 2000; Rokni and Hochner, 2002; Nesher et al., 2019).

2.4.1 Sensing and Perception

The octopus's distributed nervous system supports a complex chemotactile system within its arms and suckers. Each sucker contains a dense array of mechanical and chemical receptors, estimated at a density of several tens of thousands of receptors on a sucker 3 mm in diameter (Graziadei, 1965a). By comparison, the human fingertip has a few hundred mechanical receptors in a similar area (Johansson and Vallbo, 1979).

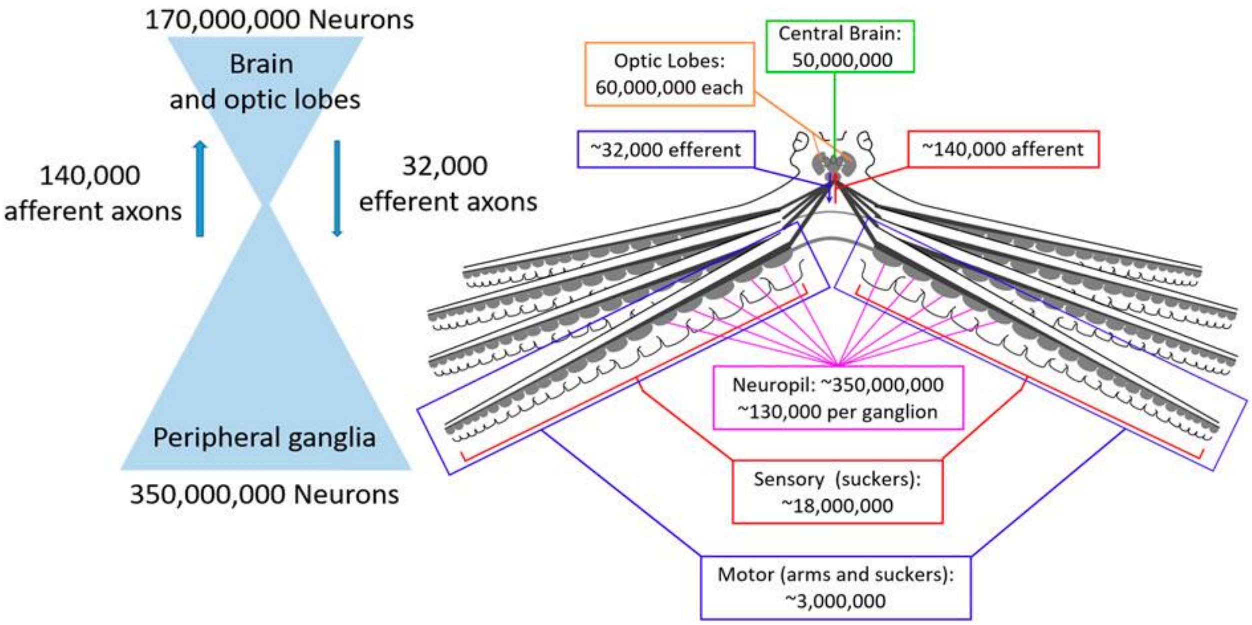

Figure 2.1. Numbers of neurons and axonal connections in the octopus nervous system. Left: The octopus nervous system is composed of two large populations of neurons, the central brain (optic lobes and brain, 170 million neurons) and peripheral ganglia (350 million neurons) that are connected by orders of magnitude fewer neurons (140 thousand afferent and 32 thousand efferent), creating a bottleneck that requires enormous compression of sensory and motor signals. Right: Numbers for each component of the nervous system on an anatomical diagram.

Chemoreceptors are the most abundant of these receptor types, outnumbering the other cell types by a factor of ten (Graziadei, 1965a). These cells aggregate along the rim of the sucker disk, where they are appropriately placed for contact with dissolved substances in the surrounding water. Chemical information is transmitted to higher neural centers after ascending through multiple levels of integration (Graziadei and Gagne, 1976).

While the outer rim of the sucker is specialized for the transduction of chemical information, the sucker disk is specialized for transduction of mechanical information, including texture, shape, and perhaps the integrity of adhesion (Graziadei and Gagne, 1976).

Information acquired by the suckers have been shown to follow two primary pathways (Rowell, 1963; Rowell, 1966; Altman, 1968; Gutfreund et al., 2006; Zullo etion al., 2011). These pathways run through the neuropil between the ganglia and through the axonal tracts.

The pathway through the neuropil seems to carry information proximally and distally, and transmit information from the sucker sensory fields and proprioceptive information from local musculature between brachial ganglia (Young, 1963). This pathway is evidently polysynaptic, such that information along this pathway is subject integration with other sources of sensory and motor information. This pathway seems to be able to relay signals over long distances of the arm provided intermediate ganglia aid in propagating the signal (Altman, 1968).

The neuropil pathway likely supports the ability of suckers to recruit their neighbors. This recruitment behavior, retained in isolated arm preparations (Rowell, 1963; Altman, 1968; Gutfreund et al., 2006; Zullo et al., 2011), enables sensory input to a given sucker to result in neighboring suckers and musculature bending toward the activated sucker, an effect which can propagate along the arm if these neighboring suckers are likewise activated. This mechanism has several advantages that we will discuss throughout the text.

The second pathway along the axonal tract seems to also transmit information proximally (Zullo et al., 2011) and distally (Rowell, 1966). The proximal signal appears to carry information to the brain while the distal-traveling signal is believed to recruit the distal arm toward proximal stimuli (Rowell, 1966). Rowell (1966) reports a considerable range of spatial representation and sensitivity among the afferent units in this pathway (Rowell, 1966). Some units responded to input to single suckers, while others responded to input to all suckers or specific groups of suckers.

The extreme sensory compression that occurs from ganglia to brain suggests that the ganglia may actively filter sensory input to determine which signals reach the brain. Since stimulus relevance depends on context, such as ambient fluid turbulence or substrate irregularity, the peripheral network may contain a mechanism of normalization by which sensory input is weighted proportionately to the global level of input for the entire animal. A rock encountered on a flat surface, for instance, would be more likely to induce a behavioral response than a rock encountered on a rocky surface. A possible mechanism to accomplish this could be a mutually inhibitory signal sent between suckers that is proportionate in strength to the level of stimulation of the suckers. This could serve as a useful mechanism to work in parallel to sucker recruitment to determine and prioritize the most relevant information encountered by the suckers.

2.4.2 Proprioceptive Information Is Locally Integrated in Ganglia

Octopuses possess multipolar cells that resemble muscle receptors seen in other species (Graziadei, 1964). While proprioceptive information about local movement and muscle position is found within the ganglia, this information, including the relative position of the suckers, has not been demonstrated within the afferent pathways in the axonal tracts or the brain (Wells and Wells, 1957; Wells, 1964; Rowell, 1966). Wells (1964) suggested that mechanical transduction occurs through the degree of distortion of the suckers upon a surface and regularity of the surface's texture. It is possibly due to this mechanism that the octopus is not able to distinguish orientations of textures and the octopus's ability to distinguish simple three-dimensional shapes is inhibited by cutting grooves into their surface (Wells, 1964). The axonal tract evidently does not communicate autonomous movement by the suckers or the arm (Rowell, 1966). Wells also found evidence that octopuses failed to learn to discriminate the weight of objects handled by the arms (Wells, 1961), suggesting that this information is also absent from the higher neural centers.

Despite these findings, Gutnick et al. (2020) showed a form of proprioceptive learning based on octopus's increased preference in reaching for the rewarded side of a confined two-choice arm maze, suggesting that the brain has some representation of and control over the directionality of the arm during extension (i.e. the arm's horizontal and vertical angle or yaw and pitch) without visual information. Octopuses can also learn to open jars containing a food reward more efficiently over multiple trials (Fiorito et al., 1990) and adapt their feeding technique with clams through trial-and-error (Anderson and Mather, 2007), suggesting the retention of some proprioceptive information from this kind of task.

Proprioceptive information is evidently exchanged between arms through the interbrachial commissure (Graziadei, 1965b; Altman, 1968), revealing a potentially important role of this pathway in the arms' ability to coordinate during movement. This is especially interesting given that this information is largely absent from the brain.

2.4.3 Action Selection

In “sense, plan, act” models motor signals would originate centrally and precisely control movement. However, rather than generating motor output as specific patterns of muscle activation, the central brain of the octopus seems to broadly transmit general behavioral programs (Zullo et al., 2009). While behaviors are seemingly decided in the brain, the motor circuitry for executing these behaviors exist within the arm nerve cords. The details of where and how to execute these behaviors may then be locally determined by integrating mechanical, chemical, and proprioceptive information within the brachial ganglia (Zullo et al., 2019). Consistent with this model, motor pathways within the arms are largely autonomous. Reaching, sucker adhesion, probing, recoiling from aversive stimuli, and sucker recruitment can all be readily evoked in arms separated from the brain (Rowell, 1963; Graziadei, 1965b; Rowell, 1966; Altman, 1968; Sumbre et al., 2001; Gutfreund et al., 2006; Zullo et al., 2011; Hague et al., 2013; Katz et al., 2021) and movement in these isolated arms kinematically resembles that seen in whole animals (Sumbre et al., 2001).

This peripheral organization of motor circuitry bears some resemblance to the spinal cord in vertebrates. Here neural circuits responsible for rhythmic movement such as locomotion, and reflexes which, for example, lead to avoiding tissue damage and maintaining posture, can operate with little to no intervention from the brain (Lemon, 2008). On the other hand, an adaptation unique to primates of a monosynaptic pathway from the motor cortex to densely organized motor neurons allows for a unique capacity for dexterity among their hands and fingers (Pearson and Gordon, 2013). This example is seemingly antithetical to the organization of the octopus, for which efferent pathways from the brain appear to innervate large pools of motor neurons along

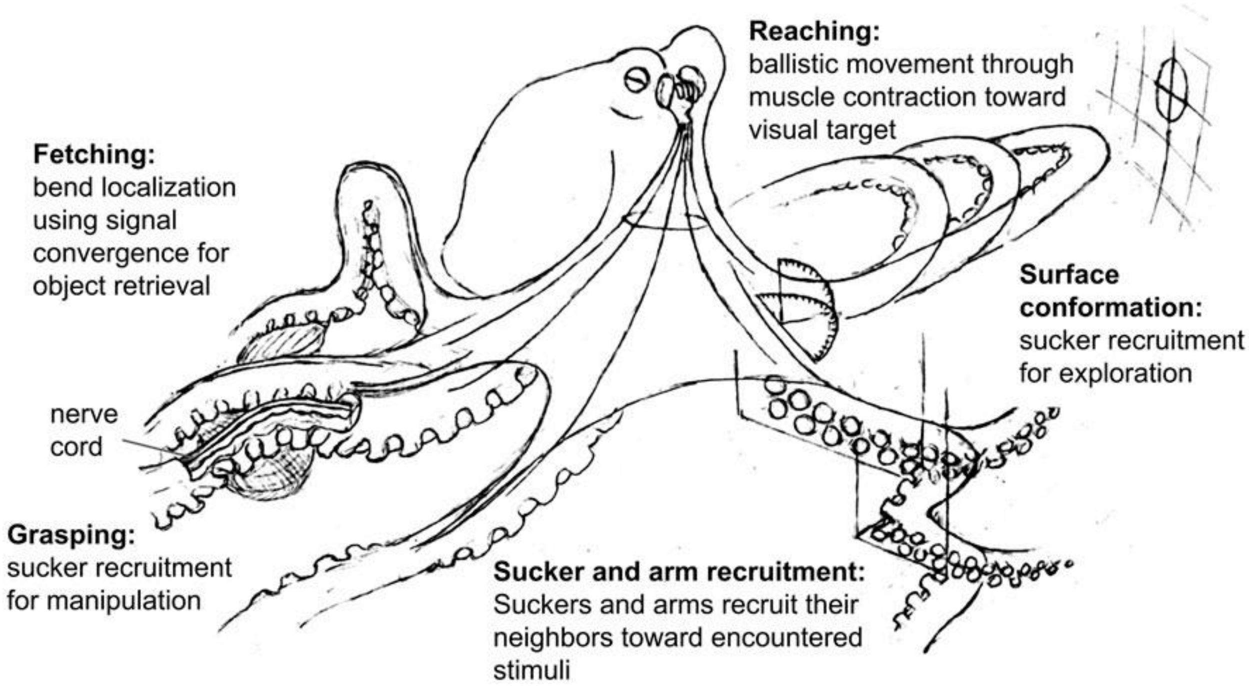

Figure 2.2. Octopus arm control strategies. Fetching: from the base of the arm, an outbound wave of muscle activation converges with another inbound wave determined by the location of the object (Sumbre et al., 2006). Arm musculature is activated at this midpoint, bending the arm appropriately to pass the object proximally. Sucker recruitment: in response to a stimulus, suckers recruit their neighbors to bend toward this stimulus. These suckers can then recruit their neighbors as this mechanism continues down the arm (Rowell, 1963; Altman, 1968; Gutfreund et al., 2006; Zullo et al., 2011). Arm recruitment: in response to stimulation of one arm, the corresponding suckers on neighboring arms orient toward the site of stimulation (Graziadei, 1965b; Altman, 1968). Grasping: as suckers collectively adhere to an object, sucker recruitment provides multiple afferent pathways for sensory input and multiple efferent pathways for manipulation. If the suckers find prey during foraging, the suckers will recruit their neighbors to capture and immobilize the animal (Rowell, 1963; Altman, 1968; Gutfreund et al., 2006; Zullo et al., 2011). Surface conformation: as suckers recruit their neighbors toward encountered surface features, the arm’s shape conforms to that of the surface (Altman, 1968; Kennedy et al., 2020). Reaching: using visual information the brain determines the horizontal and vertical angle (yaw and pitch) of the arm. The arm then extends by a wave of muscle contraction resembling a propagating bend toward the visual target (Gutfreund et al., 1998; Sumbre et al., 2001; Richter et al., 2015).

the length of the nerve cord (Zullo et al., 2019). The differences in degrees of freedom, stereotypy, feedforward versus feedback activation, generation of rhythmic movement, the role of top-down and bottom-up modulation, and the levels of polysynaptic integration present interesting points of comparison between these two control systems that we hope will be explored in depth in the future.

During the generation of movement, the octopus brain appears to send signals to the nerve cords that activate the motor circuits for different behaviors (e.g. reach, fetch, reject), and these behaviors may then be modified based on peripheral sensory information. For example, bend propagation (see Figure 2.2) has been shown to begin mid-way down the arm if the arm is reaching through a narrow opening (Richter et al., 2015), and the bend location during fetching behavior is seemingly determined by where the object of interest is along the arm (Sumbre et al., 2006). The amount of information that these behavioral signals carry with them appears to vary between behaviors. The reaching signal, for example, seems to include yaw and pitch of the arm (Gutfreund et al., 1998; Sumbre et al., 2001; Gutnick et al., 2020) while behaviors that are retained in isolated arms, such as sucker recruitment, may rely primarily on sensory feedback from the suckers and require less information from the brain. Recent work has shown efferent pathways of the axonal tract making broad, non-specific contacts with ganglia along the arm, supporting the idea that the brain does not precisely control specific segments of the arms (Zullo et al., 2019). The control of sucker movement and adhesion is also a local operation of the peripheral ganglia, though is subject to broad, top-down regulatory signals from the brain that are not directed to specific suckers (Altman, 1968). Together, this evidence suggests that the brain is limited in its ability to precisely control the arms, and relies on behaviors that are coordinated locally within the arms with minimal feedback from the brain. Figure 3 summarizes the examples of these behaviors that have been described. We predict that the brain may initiate and recall combinations of behavioral signals that lead to more complex sequences of behavior, such as manipulation (Fiorito et al., 1990; Anderson and Mather, 2007).

Fine-scale local control through sucker recruitment (section below) enables precise grasping and manipulation of objects when they are encountered by the suckers. As suckers are recruited to collectively adhere to an object, the control the arm has over the object is compounded. Through locally recruiting suckers to interact with an object, this mechanism adaptively scales the number of afferent pathways for sensory information and efferent pathways for manipulation, all without precise central control.

2.4.4 Locomotion

Despite the limited bandwidth through which the brain and arms communicate, the arms together demonstrate remarkable coordination during locomotion (Levy et al., 2015). This movement is independent of the orientation of the body: the octopus can change direction of crawling without changing orientation of its body and vice versa. Although arms were found to individually generate rhythmic patterns of movement, the pattern between arms showed no obvious consistency. The octopus appears to lack the rhythmic motor output that characterizes central pattern generator-driven locomotion of other animals. The recruitment of the pushing movement in the arms to generate locomotion may result from a moment-to-moment pattern of activation from the brain, allowing the octopus to immediately adjust its direction (Levy et al., 2015).

Coordinated behavior between arms has been shown to be retained following isolation from the brain (Graziadei, 1965b; Altman, 1968), and severing an arm’s connections to the interbrachial commissure has shown to affect the arm's ability to coordinate with the other arms during locomotion (Altman, 1968). These observations suggest that the peripheral nervous system is to some degree responsible for coordinating arm behavior. The interbrachial commissure, which connects the nerve cords into a ring, is the primary pathway by which information from the arms bypasses the brain (Altman, 1968) and information carried by the interbrachial commissure evidently includes a representation of the spatial arrangement of the arms (Graziadei, 1965b; Altman, 1968). These findings suggest that this pathway may play an important role in the ability of the arms to work in cooperation during complex behaviors, including the pattern of arm recruitment during locomotion.

2.5 Octopus-Inspired Robotics

While, like any natural system, there is a considerable nuance to the octopus's control system, we would like to propose three broad control strategies that the octopus appears to be employing, and which are applicable to the current field of robotics: hierarchical hybrid action selection, used as a top-down control strategy, ascending recruitment, used as a bottom-up control strategy, and contact-based navigation and manipulation which emerges from recruitment.

2.5.1 Hierarchical Hybrid Action Selection

The octopus controls a soft body with a large number of passive degrees of freedom, complex musculature, and highly concentrated sensory fields. We propose that this control problem is simplified by organizing motor commands into a hierarchical structure of action selection (Zullo et al., 2009; Merel et al., 2019), thereby reducing the state space to manageable levels. As the high-level controller, the brain of the octopus selects from among actions over a discrete domain. The brain then sends a general signal to the peripheral network of ganglia, which is composed of subordinate semi-independent agents (the ganglia). These agents then select from a subset of actions (local motor control) over a continuous domain as defined by the action decided by the brain, similar to hybrid control strategies (Branicky et al., 1998). Figure 2.3 illustrates this form of control in the octopus. The control problem inherent in the octopus's large number of degrees of freedom could be further simplified by relying on feedforward movement strategies in unconstrained (high-dimensional) conditions (e.g. reaching toward a visual target (Sumbre et al., 2001), and feedback strategies when operating in a lower-dimensional constrained environment (Gutnick et al., 2011), in which the arm can use the mechanical and chemical composition of its surroundings as a reference [e.g. searching through crevices (Mather and O'Dor, 1991; Forsythe and Hanlon, 1997)]. It is tempting to identify exploration as the default motor strategy of the arms based on observations of denervated arms readily engaging in probing and sucker recruitment. These mechanisms may be overridden in favor of locomotory behaviors.

Hierarchical control has been suggested as a general framework for the control of complex systems (Barto and Mahadevan, 2003), and the octopus is an exemplar of this form of control (Zullo et al., 2009; Wayne and Abbott, 2014). While hierarchical control theory is an attractive framework for understanding motor control across numerous species (Merel et al., 2019), a striking feature of the octopus is that the putative levels of hierarchical control are physically separated and connected by distinct axonal pathways.

2.5.2 Ascending Recruitment and Contact-Based Control

Sucker recruitment serves as an effective mechanism in foraging, exploration, and manipulation. We propose that by relying on this simple sensory-motor reflex across such a breadth of behaviors, the octopus can simplify the control of its highly flexible arms.

Suckers that encounter a stimulus recruit unoriented suckers, and in conflicting situations where two or more stimuli are recruiting a shared set of suckers, presumably the stronger stimulus will send the stronger signal and override the competing stimuli. Although unknown, a mechanism for such "winner-take-all" sucker recruitment could be realized by a mutually inhibitory signal sent between suckers proportionate to the strength of the stimulus that they have encountered.

The suckers may therefore act as an adaptive sensory filter by locally prioritizing stimuli, providing a peripheral mechanism for determining which signals are sent across the narrow bandwidth through which the brain and the arms communicate. While the representation of a stimulus encountered by a single sucker is limited in higher neural centers, a stimulus that successfully attracts the attention of multiple suckers by eliciting a recruitment signal would be represented through multiple afferent pathways. Engaging multiple suckers with a stimulus both maximizes the amount of information acquired from the stimulus and the amount of control the suckers have over it. Spreading sucker recruitment could also determine which of the suckers on a given arm act as the end effectors during manipulation and locomotion. This mechanism also works as an effective hunting strategy: if a sucker finds prey, it will recruit its neighbors to efficiently capture and immobilize the animal. This may be particularly effective if the less prominent distal suckers find prey and recruit larger proximal suckers to aid in capture. This mechanism can additionally benefit foraging by conforming the arm to surface features of the

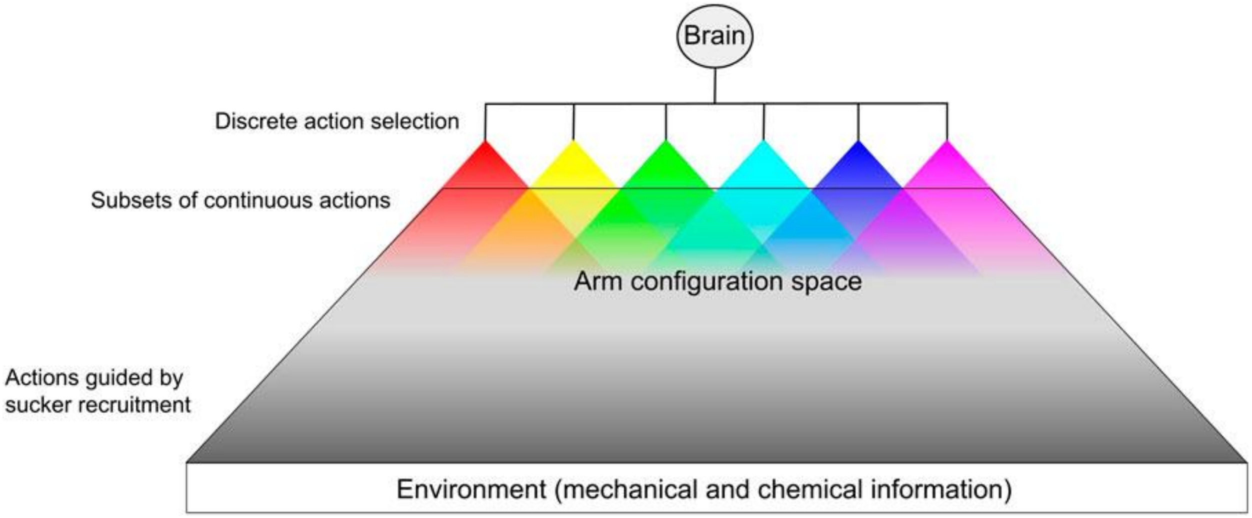

Figure 2.3. Hypothetical pipeline of hybrid hierarchical action selection. For each arm, the brain determines an action over a discrete domain (e.g. fetch, reach, push, reject, etc.). For each discrete action, the arm is allowed a subset of continuous stereotyped actions executed based on peripheral proprioceptive information and sensory information from the environment. The actuation of these continuous action subsets overlap within the arm's configuration space. Most of the arm's configuration space is dominated by the possible arm shapes resulting from sensory-guided sucker recruitment (e.g. surface conformation). Some behaviors, such as reach, have some continuous parameters that the brain may be able to set (Gutnick et al., 2020).

environment. In this case, recruitment could lead the arm around corners or into crevices to find prey (Mather and O'Dor, 1991; Forsythe and Hanlon, 1997), enabling an exhaustive search over even the most complex surfaces. See Figure 2.4 for an example of sucker recruitment during food detection and retrieval.

Traditional robotics expends a great deal of computation to avoid collisions with obstacles. The vast configuration space of the octopus arm appears to compound this problem, providing a nearly infinite number of configurations for which a collision with environmental features must be considered. However, behavioral and neural evidence suggests that the octopus avoids this seemingly intractable computational problem; instead, the octopus's reliance on contact as a result of sucker recruitment could simplify its control strategy, mechanically restricting its configuration space to the contraint manifolds defined by obstacles, dramatically reducing the computational complexity of its control scheme.

Two additional varieties of sensory input have been shown to possibly restrict the arms' degrees of freedom. Nesher et al. (2014) discovered that a chemical in the octopus's skin prevents the suckers from attaching to it. This mechanism is evidently peripheral—it is retained in the arms when severed, but can seemingly be overridden by the brain when the arms are left intact. Katz et al. (2021) found that arm tips reflexively withdraw from light, a response which is likely mediated by the brain but acts independently of visual feedback. Both chemical and photosensory feedback therefore seem to play a similar role as mechanical input in limiting the arms' range of possible configurations.

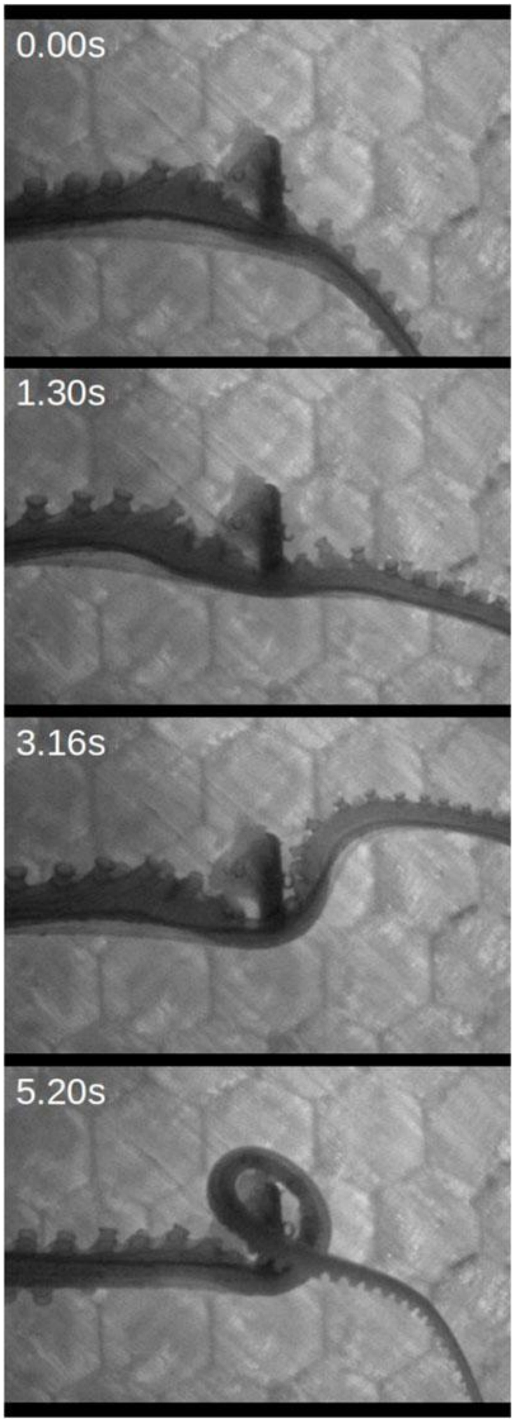

Figure 2.4. Sucker recruitment used to grasp shrimp meat during foraging. Consistent with localized spread of sucker recruitment, orientation and movement of suckers towards the food occurs in waves propagating from the point of food contact.

Graziadei (1965b) and Altman (1968) noted that stimulation of one arm will cause the nearest arm to turn toward the site of stimulation, even without innervation from the brain. This represents a possible second level of recruitment (Byrne et al., 2006) that could result in the same benefits of sucker recruitment. Recruitment of neighboring arms, like that of the suckers, could rally multiple effectors for handling objects and immobilizing prey, and compound the strength of the afferent signal communicated to the brain. The brain could then update the motor plan across multiple arms based on this locally-filtered and amplified signal. The pathway through the brain provides an additional means by which suckers may recruit each other. In this case, the brain may be considered another recruitable winner-take-all node in this ascending recruitment mechanism that influences behavior across the entire network by generating a renewed motor plan. At this level, additional factors such as visual information, memory, and internal state also contribute to updating the motor plan.

Afferent pathways within the arms carrying mechanical information are fast adapting and habituate quickly to unchanging stimuli (Rowell, 1966). Dynamic mechanical stimuli are thus preferentially communicated between ganglia and along the axonal tract to the brain. Novelty, possibly representing fluid motion, surface irregularity, or prey movement, could therefore serve as a strong ascending recruitment signal across the hierarchy of the octopus nervous system. This may represent a neural mechanism for the notable curiosity the octopus displays (Mather and Anderson, 1999; Kuba et al., 2003; Kuba et al., 2006a; Kuba et al., 2006b), and the motivational connection between exploration and foraging (Kuba et al., 2006a). The octopus's nervous system supports seeking out and assessing the novelty of information in the environment, which is an area of active research in robotics (Grizou et al., 2020). We suggest it is appropriate, therefore, that particular attention is given to the octopus in the design of robotics for the purposes of exploration, with application to projects such as the Honda Curious Minded Machine program.

2.6 Lessons From the Octopus for Robotics

An underactuated robot hand can bring multiple joints into a configuration that closely mirrors the object's geometry, despite not having enough control degrees of freedom to generate this pose in the absence of the object. Octopuses appear to make even more extensive use of under-actuation and compliance: they are underactuated at both the mechanical level and the control level. Mechanically, the body of the octopus is highly compliant, enabling it to conform to complex geometries with computationally simpler control than would be required for active control of non-compliant mechanisms.

Unlike most rigid robots, which are usually programmed to avoid collisions with obstacles, the octopus arm appears to seek out contact with surfaces or other nearby objects. We hypothesize that contact with external rigid objects allows the arm to localize itself with respect to the environment. This is similar to a strategy called coastal navigation that has been employed in mobile robotics to reduce positional uncertainty (Roy et al., 1999). Due to the arm's many passive degrees of freedom (i.e. its mechanical compliance), the same set of motor commands resulting in sucker recruitment can cause the arm to conform to a large number of different surface geometries. Thus one simple motor program could potentially produce arm shapes that mirror a wide variety of surfaces.

The reliance on contact with the environment, its local distributed control of suckers, and a highly compliant body, enables the octopus to accomplish complex behaviors using much less computation than would be required by a brute force sense-plan-act approach to planning and control for its large number of actuated degrees of freedom. The octopus generates motor commands via a hierarchical process, with higher level motor commands originating in the brain and lower level closed loop control processes occurring at the suckers. At the lowest, mechanical level, the octopus makes use of underactuation via its highly compliant body; this is analogous to some work in underactuated hands, and soft robotics. The local control of suckers, including recruitment, appears to be an intermediate strategy between passive mechanical compliance and global computational planning that may be the most novel compared to conventional robotics. While it is common for robots to use a slower planning process to choose position, velocity, or torque commands for joints, and faster control loops to implement those commands while rejecting disturbances, the octopus has a more complex layer of distributed, local control, which allows it to control thousands of actuated degrees of freedom, namely the sucker and arm musculature. The octopus's highly capable distributed control layer appears to be quite distinct compared to conventional robotics. Even though it is not possible today to build a robot with as many locally controlled degrees of freedom as an octopus, the architecture of the octopus could be implemented today in a robot with a smaller number of locally controlled degrees of freedom. Achieving a better understanding of the functional capabilities provided by the octopus's hierarchical control scheme, as well as understanding the limitations of its local distributed layer, suggests new approaches to planning and control of robots, approaches which have the potential to provide more capability with less computation.

Chapter 3. Mechanisms of octopus arm search behavior without visual feedback

3.1 Introduction

The octopus employs its eight highly flexible arms across a range of behaviors, including foraging, exploration, manipulation, and locomotion. Each arm has hundreds of suckers staggered along its length. These suckers bear a complex chemotactile system (Graziadei, 1964; Graziadei & Gagne, 1976; Graziadei, 1965a; van Giesen et al., 2020) and are the primary appendages used by the octopus to interact with its environment (Packard et al., 1988). Most of the octopus's nervous system is distributed into its arms and suckers (Young, 1971), and locally controls behavior with minimal feedback from the brain. Much of the arm's behavioral repertoire therefore remains intact when the arm is denervated from the brain (Gutfreund et al., 2006; Altman, 1968; Rowell, 1963; Zullo, 2011; Sumbre et al., 2001).

The brain and arms communicate over a limited neural bandwidth (Young, 1965) and a great deal of information within the arms, such as proprioceptive information from stretch receptors in the arm musculature, has been found to not be communicated to the brain (Rowell, 1966; Wells & Wells, 1957; Wells, 1964; Graziadei, 1965b). With a limited representation of the configuration of the arms and suckers, the brain is likewise limited in its ability to generate a detailed motor plan. Instead, it has been suggested that the brain sends out a generalized motor plan to the arms, where it activates peripheral neural circuitry to locally control behavior under the direction of the suckers' complex chemotactile system (Zullo et al., 2009; Zullo et al., 2019). This reliance on local control in place of centralized planning means that the brain is also limited in its ability to recall the details of arm behavior (Wells & Wells, 1957; Wells, 1964).

Possibly due to the lack of sensory feedback from the arms, reaching behavior relies on a feedforward activation mechanism (Gutfreund et al., 1998; Sumbre et al., 2001), which gives the arm a ballistic kinematic profile as it extends toward its target. This suggests that the brain only takes into account the vertical and horizontal angle (yaw and pitch) of a target and activates reaching behavior in this direction without any further modification of the behavior following its activation. Where this information is sufficient for the retrieval of a reward, the octopus shows an improved performance over time without visual feedback (Gutnick et al., 2020). Beyond these limited parameters that the brain is able to control and recall, the suckers and their local nervous system likely provides the necessary sensory-motor feedback to adapt behavior to the environment.

In tasks where visual feedback is absent and feedforward activation is inadequate for the retrieval of a reward, the octopus must rely primarily on the chemotactile system of the suckers in the generation and modification of behavior. Characterizing the strategies that are employed by the arms and suckers to search for and retrieve a reward in the absence of visual feedback can therefore help resolve how the chemotactile system is used to control the arm's extreme flexibility. Here, we investigate the strategies used by the Pacific red octopus (*Octopus rubescens*) when searching for and retrieving a food reward from a visually occluded foraging task space.

Previous studies have described a locally controlled behavior within the arm which we refer to here as sucker recruitment. During this behavior, which can be elicited when the arm is denervated from the brain, sensory input to a sucker results in the neighboring suckers bending toward the source of this sensory input (Gutfreund et al., 2006; Altman, 1968; Rowell, 1963; Zullo, 2011). This same effect can then be elicited in these neighbors and cause a propagating wave of recruitment down the arm. This recruitment mechanism can serve as an effective strategy for object handling and prey capture, and could likewise serve as a potential foraging strategy by allowing the arm to adapt to the shape of complex surfaces in search of prey hidden within unseen crevices. This form of surface conformation could further provide a means for the octopus to simplify control of its movement by providing constraints on the arm's vast degrees of freedom. The reliance on contact would be consistent with a force control (rather than position or velocity control) strategy by the octopus.

We therefore predict that if the octopus reaches its arm through a narrow entrance into an open space, sucker contact with the entrance will initiate a recruitment signal which will attract the arm toward the surfaces of the space shared by the entrance. We also predict that the arm will preferentially search along concave edges and vertices where multiple surfaces meet, as these contours could serve to confine the arm's range of possible configurations and thereby simplify behavior.

To investigate the role of sucker recruitment in generating our experimental observations, we created a simple computational model of the octopus arm and subjected it to simulated experimental conditions that precisely matched our 3D-printed experimental task space. This model included a recruitment mechanism that could be activated between serially joined segments, which operated in parallel to random motion generated within the joints. This random motion was amplified at the proximal-most joint of the model, which corresponded to the section of the octopus's arm reaching through the task entrance.

3.2 Methods

Subjects for this study included eight Pacific red octopuses (*Octopus rubescens*) collected using SCUBA from the Puget Sound. All animals were collected under an approved permit through the Washington Department of Fish and Wildlife. Animals were kept in tanks that ranged in volume from 3 to 40 gallons (roughly 10-150 liters) depending on the size of the animal, tank availability, and enrichment schedule. During the course of the study, the subjects were offered food (scallop or shrimp meat) equal to 1-2% of their mass daily as the reward for the task. All animals were enriched and handled regularly during the course of the experiment. All experiments were carried out in accordance with a protocol approved by the University of Washington Institutional Animal Care and Use Committee (IACUC).

Figure 3.1 outlines our experimental design. The foraging task and its interior task space were created using computer-aided design (CAD) software and 3D-printed with white polylactic acid (PLA) filament. This task was secured to the side of a glass or transparent acrylic tank using magnets, such that the task space was visible to a camera outside the tank, but visually occluded to the octopus. At the top of the task was a circular entrance large enough for a single arm to fit through. This entrance was at the bottom of a larger opening designed to guide the octopus's arms toward the entrance. The task space was shaped as a half-cylinder that connected the entrance on its upward-facing round side to a rectangular box on its downward-facing flat side. The box and half cylinder had the same depth along the axis between the tank and the camera. The task was printed in two sizes depending on the weight of the subject. Octopuses over 80g were assigned the large task and octopuses under 60g were assigned the small task, which was 80% the size of the large task. Octopuses between 60-80g were randomly assigned to either version. A light was used to illuminate the task from behind to maximize the contrast between the task space features and the octopus's arm. An acrylic barrier prevented the octopus from

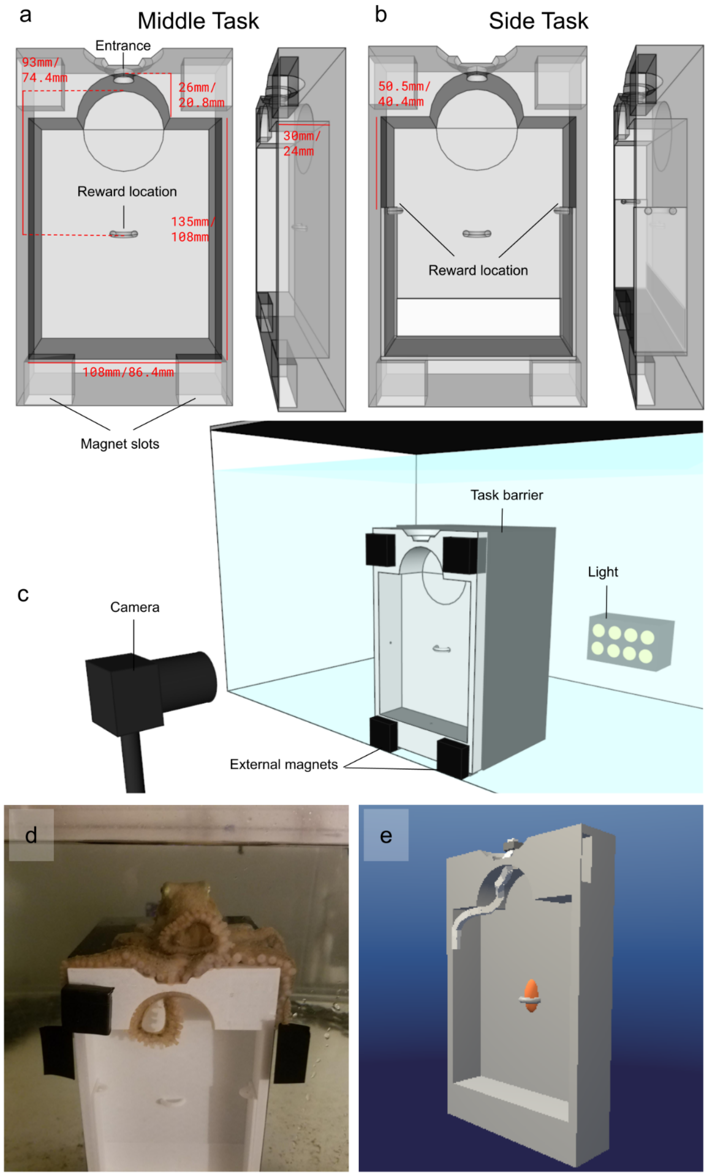

Figure 3.1. Experimental Design. (a) Middle and (b) Side task CAD design with dimensions of both large and small task versions displayed. (c) Experimental setup. (d) Octopus during attempt. (e) Model arm during simulated task.

creating shadow artifacts by reaching between the task and the light. Prior to the start of trials, the octopuses were trained to approach the entrance of the task for a food reward while the interior was blocked off.

For one condition ("Middle" ; n = 4 males), the food reward was secured in the center of the box's largest face, and in the other condition ("Side"), the reward was secured to either the left (n = 2; one male and one female) or right wall (n = 2; one male and one female) of the box close to the concave edge between the wall and the box's largest face. Video recording failed for the first trial of one subject in the side condition, so this trial was not included in the analysis. The reward was equally distant from the entrance in both conditions.

The octopuses were given as many opportunities as needed to retrieve the reward six times from the task. Each of these six trials included the total time the octopus spent searching the task space until the reward was found. The time between when an arm entered the task space and when it either found the reward or left unsuccessfully was considered an attempt. Trials often consisted of multiple failed attempts before a successful attempt was made. Arm behavior was recorded at 250 FPS with a CMOS camera (Imaging Source, model DMK 37BUX287) and custom-written software in LabVIEW (National Instruments). Arms were tracked using DeepLabCut pose estimation software (Mathis et al., 2018), and analysis was performed using custom routines written in Python.

The computational model was developed using the Unity game engine as a chain of rigid body segments connected by joints with three degrees of freedom (yaw, pitch, and roll). The mechanics of the arm were written as routines in C# and performed two primary functions. One of these was to simulate sucker recruitment in response to contact with environmental features.

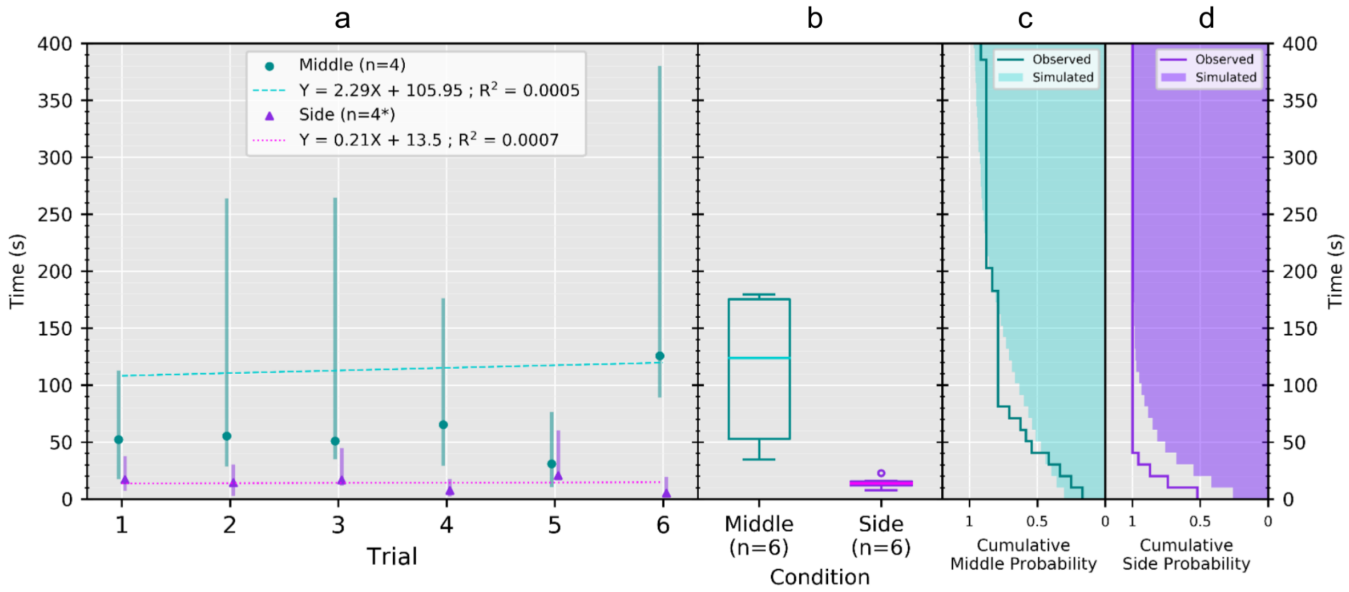

Figure 3.2. Performance as time to success. (a) Performance over trials (as median and interquartile range), and regression showing no improvement. (b) Performance between conditions as trial averages, showing significantly better performance for the side task (Mann-Whitney *U*; $p < 0.05$). (c) Middle cumulative probability distributions of observed and simulated performance, showing shared distribution (K-S; $p = 0.21$). The maximum observed and simulated trial duration lasted 604.34 and 916.56 seconds, respectively. (d) Side cumulative probability distributions of observed and simulated performance, showing discrete distributions (K-S; $p = 0.01$). *Video recording failed during the first trial of one subject in the side condition, so this trial was not included in the analysis.

Upon touching a surface, torque was applied to the neighboring segments to rotate them in the direction of the feature. This caused the arm to conform to surface features as each segment propagated this recruitment signal in response to touching the feature. The second function was to generate random motion of the arm. This took the form of a random intensity of torque from a range applied to each segment in a random direction along the yaw and pitch of its proximal joint after a randomly selected delay between two and three seconds. The intensity for the proximal-most joint, connecting the segment reaching through the entrance to a stationary segment just outside the entrance, was 20x that of the other joints. The segments were also subjected to a drag force to simulate motion through liquid. The task was simulated by importing the task CAD file into Unity. The arm began each trial in a straight vertical pose extending down from the entrance. A simulated trial was completed when the arm made contact with the reward, which approximated the size and shape of the food rewards from the experiments.

3.3 Results

Performance for the observed data was assessed based on the time taken to reach the reward over the six trials and between the two conditions (time to success, Figure 3.2). There was no improvement in performance across the six trials for either condition, but there was notably consistently better performance on the side task across trials. When trial averages were compared between conditions, the octopuses performed significantly better on the side task (Mann-Whitney U, $p < 0.05$).

Three kinematic measures were used to characterize arm behavior during the octopus's attempts to find the food reward: arm segment speed, curvature, and wall proximity (Figure 3.3). All three of these measures showed a recurring behavioral profile represented by a distally

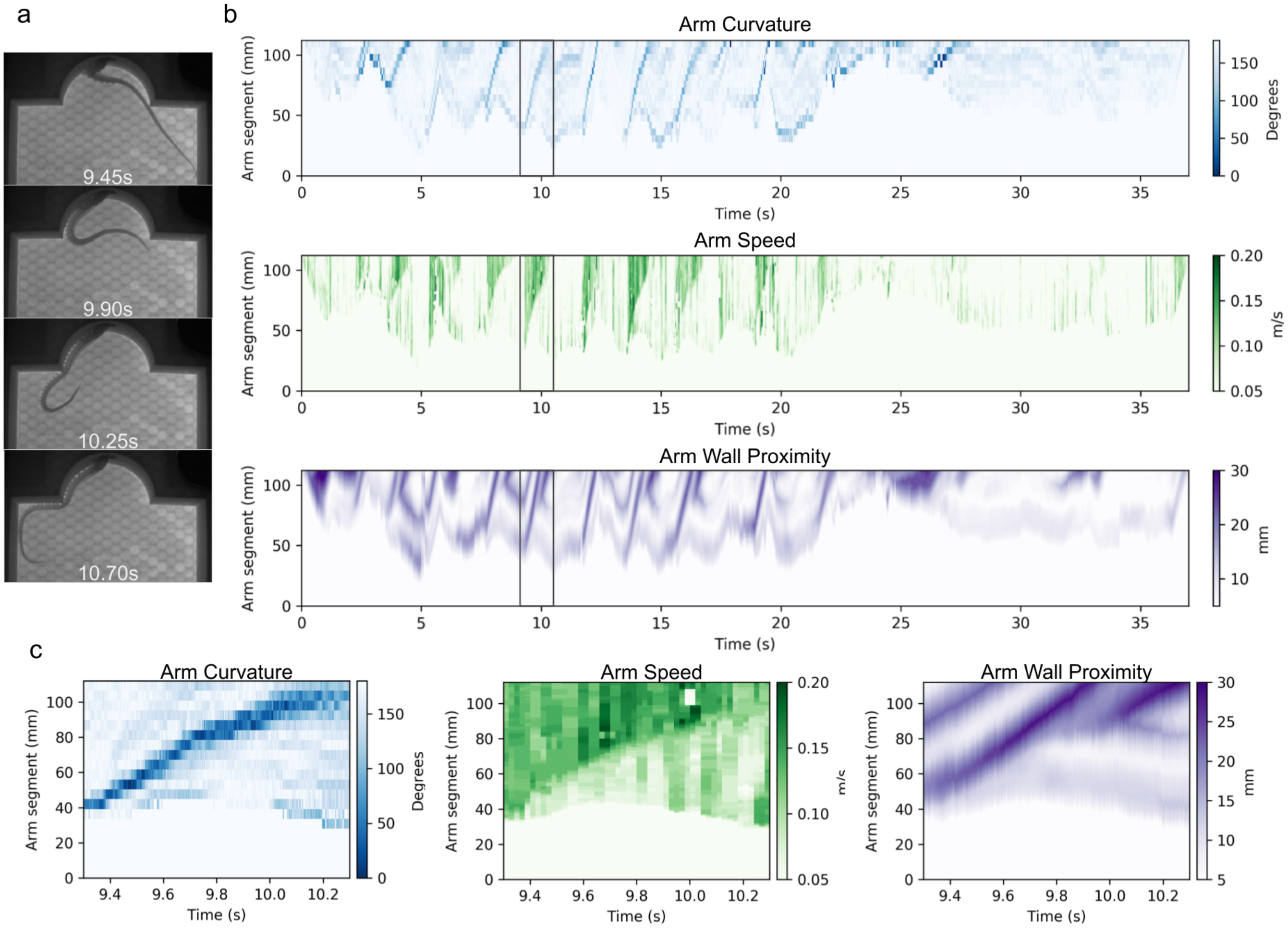

Figure 3.3. (b) Example timeplots representing arm curvature (top), speed (middle), and wall proximity (bottom) during a middle attempt using the large version of the task. Horizontal axes represent time and vertical axes represent segments of the arm with the arm tip at the top. (a & c) Recurring kinematic profile of a propagating wave of curvature, deceleration, and movement toward the wall. Note that curvature is represented here by the angle between segments in degrees, such that the lower the value the greater the curvature.

oriented wave of deceleration, curvature and movement toward the wall, suggesting that the proximal arm leads the initiation of this behavior. The wave appeared to be a result of a distally propagating wave of sucker recruitment initiated and continuously regenerated by sucker contact with the task space features. This resulted in the arm conforming to the shape of these features, which was likewise reflected in arm occupancy across animals and trials (Figure 3.4), showing the arms spending most of their time conforming to the sides of the task during the experiment.

Using the model, we ran 1,000 simulations for each condition. We then compared the performance distribution for each simulated condition to our observed performance data using a Kolmogorov-Smirnov (K-S) test. Results suggest that the observed and simulated arms share a distribution for the middle task ($p = 0.21$), but not for the side task ($p = 0.01$). This shows that the model accurately simulated performance when the reward was found in the center of the task space. While the observed and simulated distribution for the side task appear to share a profile, the experimentally observed arms in this case acquire the reward consistently faster.

We ran a single simulation for 1,000 seconds to characterize the preferred occupancy of the model (see Figure 3.4). No reward was included in this simulation to prevent the model from being reset to its starting pose upon finding the reward. Like the experimentally-observed arms, the model preferred to conform to the shape of the task space features, which suggests that the model accurately simulated arm occupancy.

3.4 Discussion

To describe the control problem that the octopus faces, we will introduce the concept ‘configuration space’ used in the field of robotics to represent the multidimensional space of all possible configurations of a robot, where each axis represents a degree of freedom of the robot’s joint angles. The more joints a robot has, the higher the dimensionality of its configuration space. With the octopus arm able to bend at any continuous point along its length in any direction, the octopus's space of possible configurations is immeasurably large (Kennedy et al., 2020). This is all the more striking given that the octopus employs its arms across a wide range of behaviors. By using limbs with effectively infinite degrees of freedom across a variety of adaptive behaviors, the octopus has solved a significant control problem facing the field of soft-bodied robotics. If we can identify and characterize the biomechanical properties and control strategies the octopus employs to do this, we can implement these elements in the development of soft-robotic limbs with a similar range of capabilities.

Here we investigated the strategies that the octopus uses to search for prey without visual feedback, which is often the case when foraging within crevices, under rocks, or in conditions of low visibility. In these cases the role of vision is removed, and without a central representation of arm configuration, the octopus must rely primarily on the chemotactile feedback received by the suckers and the behaviors locally controlled within the arm's nerve cord.

To identify the mechanisms underlying these behaviors, our approach is to program these mechanisms into our computational model, subject the model to simulated experimental conditions, then compare the model's behavior to that of the octopus arm. The more accurately the mechanism is replicated within the model and the larger role the mechanism plays in the arm's behavior, the more closely the model would reasonably match the experimental data.

The prevalence of sucker recruitment in behavior with and without a connection to the brain made it a compelling mechanism to investigate within this modeling framework. As this mechanism alone would cause the model to stick motionless against a surface, we paired it with random motion generated within the segments. This motion was amplified in the proximal-most joint to simulate the proximally-led, distally oriented recruitment signal observed from the kinematic data.

Together, these mechanisms resulted in a pattern of the proximal segment "casting" the arm in a random direction, where the rest of the segments then serially conformed to the task space features. Between these larger casting motions, the random motion of the distal segments caused the arm to move laterally across the surface.

The performance and occupancy of our experimental results suggest that the arms preferentially conformed to the shape of the task space's surface features, particularly along its concave edges, and that this behavior led to greater performance when the reward was found on the side.

To isolate sucker recruitment as the underlying mechanism of this behavior, we compared the performance distributions of our experimental data with those of our simulations. This comparison indicated that the observed and simulated arm share a distribution for the middle task, but not for the side task. While observed and simulated distributions shared a similar profile for the side task, the observed arms found the reward significantly faster. There are a number of possible reasons that could explain why the octopus performed better than the model that highlight the model's limitations.

While the random motion generated a performance and occupancy profile that resembled the observed arms, the octopus likely employs a more systematic search strategy. For example, when conforming to a surface, the octopus arm's lateral movement is most likely not equally probable in both directions. Also, rather than generating larger proximal movements within a random interval of time, this kind of behavior probably occurs after the arm exhausts the novelty of a searched area. It is reasonable to suggest that these two factors are not as limiting when the reward was found in the middle, which may have accounted for the closer resemblance in performance between the model and the observed arm for the middle task.

A systematic search strategy of the arm is interesting as it implies the existence of a mechanism allowing the octopus to distinguish areas that have been searched from those that have not. This mechanism could be based on the afferent profile of mechanical novelty and other relevant cues, such as odorants, and how this profile diminishes with prolonged exposure to unchanging input. The motor response to this could take the form of lateral motion by the suckers crawling across the surface, a smaller subset of proximal suckers orienting in a new direction and causing a recruitment signal to reposition the arm, or a simple arm extension (i.e. reaching). Extension seems ineffective in the execution of a systematic search strategy as it would require the arm to lose contact with the surface, making the octopus lose all indication of its search progress given that arm configurations during the search attempt are not encoded proprioceptively.

Our model further differs from reality in that it does not take into account chemical cues. Chemical cues could inform a more directed search by the arm when near the reward, however, these were not simulated within our model. Instead, if the model comes near the reward, it is not guided by these local sensory cues. Meanwhile, the octopus's suckers are densely innervated with chemoreceptors that may be picking up both the chemical cues from a nearby food source and its relative direction (Fouke & Rhodes, 2020; Walderon et al., 2011; Chase & Wells, 1986). Both the lack of this available information to the model and its inability to conduct systematic search patterns may account for the difference in performance between the simulated and observed search efficiency when rewards are located on the side of the task space. Another possible

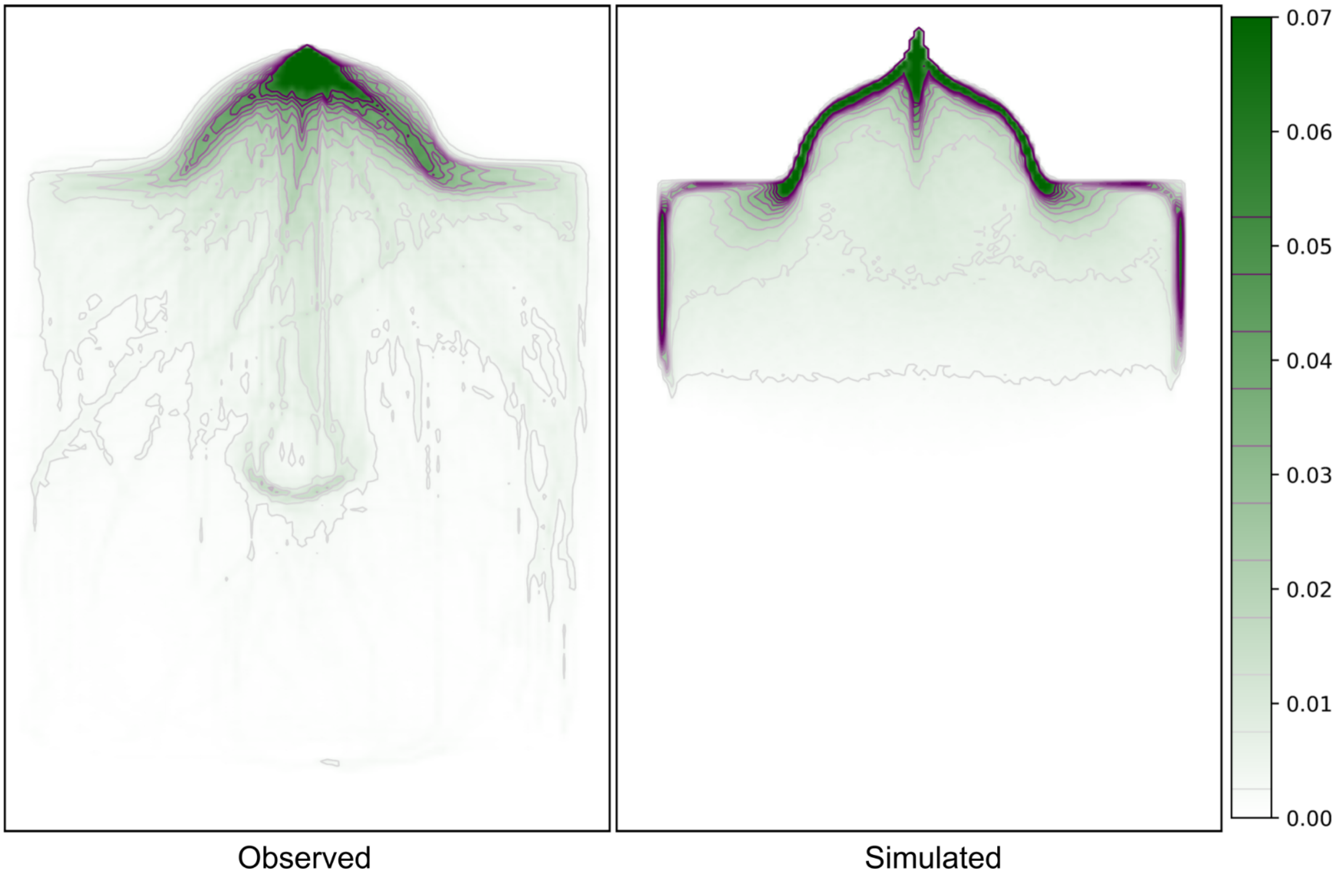

Figure 3.4. Most commonly occupied areas of the task for (left, "Observed") the observed arms as proportion of total time across all trials and all animals (equally weighted) and for (right, "Simulated") the model over 1,000 seconds of a simulation without a reward to find. Both the arms of the observed data and model in the simulated data were represented by a single pixel-width line to calculate these plots.

mechanism that combines these features could be a systematic search informed by chemical cues indicating the areas the arm has already investigated.

We attribute the difference in performance between the two observed conditions to a few primary factors. As the octopus searched the task space, the one definite location where the arm was making contact with surface features was where it was reaching through the entrance, and from this point of contact we believe a strong recruitment signal was being sent distally. Though the middle reward was secured to a surface, this surface was separated from the entrance by a concave edge oriented orthogonally to the direction of the reward relative to the entrance. The proximal-to-distal recruitment signal, likely guided by this edge, oriented the arm away from the middle and toward the side. The recurring kinematic profiles appearing in the arm speed, curvature, and wall proximity time plots reflected the prevalence of this behavior. Because of these factors, the most likely way for the arm to find the middle reward was when proximal-to-distal recruitment caused the distal arm to sweep past the reward while switching sides of the task space.

Distal-to-proximal recruitment was observed, though it usually occurred only after distal suckers found the food reward. Free proximal suckers were then “reeled in” toward the reward. This was not included in the analysis primarily because this behavior was difficult to track with DeepLabCut. This behavior indicates that while distal suckers are limited in their ability to capture and manipulate prey because of their size, they may serve as scouts by locating prey then recruiting proximal suckers to capture it.

The extent to which morphology and neuroanatomical organization is conserved across units of the sucker and its adjacent length of the arm’s nerve cord and musculature has not been fully characterized. It is therefore informative to ascertain the degree to which the octopus arm’s behavior was simulated in a model whose segments were controlled by identical routines. While it has been shown that in locomotion, separate functional roles tend to be adopted by different lengths of the arms (Levy et al., 2015; Mather, 1998; Hooper, 2015; Levy & Hochner, 2017), it seems that in the context of search behavior (and possibly other behaviors employing similar recruitment patterns), sucker-arm units may be functionally identical.

By reflexively conforming its arm to the shape of the surrounding surfaces to guide its movement, these surfaces can confine the enormous degrees of freedom of the arms to a more manageable range of configurations. Serving as a lower dimensional reference during behavior, surfaces, especially sharp concave features, appear to act as coastlines in the arm’s configuration space and are perhaps used in an analogous way as coastal navigation is used by ships (Roy et al., 1999).

This behavioral strategy based on contact with the environment is interesting, as in the field of robotics collision with environmental surfaces is generally avoided. For the soft-bodied octopus arm, rather than being avoided, collision appears to be exploited as a control strategy. However, unlike the simple architecture of our task, the surface features of the octopus's environment are convoluted and complex. The next step for this paradigm will be to investigate how this strategy is employed with tasks more closely representing this kind of surface complexity.

We believe that the number of trials used for this investigation was not sufficient to conclusively interpret the lack of improvement in task performance. However, in the event that learning is possible within this series of trials, we suggest that each condition faces its own barrier for improvement. The middle task showed no improvement because, without the arm using a surface to guide its search strategy, the brain would need to encode and recall the shape of the arms when they found the reward. However, this level of detail, namely relative position of the arm and suckers, is evidently not represented within the brain and therefore cannot be recalled to find the reward more efficiently over repeated trials. Meanwhile, the lack of improvement for the side task may represent that, as a reflex, surface conformation as initiated by sucker recruitment is limited in its capacity for improvement. However, as we mention above, there is at present a limited amount of evidence for a lack of learning; we expect that further work might provide additional evidence.

Additional limitations we would like to highlight are the lack of available females (since all animals were wild-caught, sex of animals included in the study was not under our control), and our inability to distinguish between arms with this task design (with the exception of the third right arm in males, due to the presence of the hectocotylus). The questions that we are unable to address due to this latter limitation are potential arm preference, individual arm performance, and individual arm improvement. With the results presented by Bowers et al. (2021), suggesting a possible peripheral mechanism for memory encoding within the arms of the dwarf cuttlefish *Sepia bandensis*, these are clearly interesting and viable research questions that this paradigm should seek to address moving forward. Efforts for future work will therefore be made to modify task design to be able to distinguish arms.

The paradigm we used for this investigation involved using CAD software to design and 3D print a task space that encouraged a specific behavior in the octopus. We then tracked the arm to characterize its behavioral patterns and kinematics, and developed a model of the arm equipped with mechanisms meant to generate the behaviors that we observed. Using the CAD file for the task, we were then able to simulate the experimental conditions for the model and compare the results to those of the experimental data, thus validating the mechanisms we provided the model as likely mechanisms within the octopus's arm. This paradigm presents an effective pipeline for both characterizing underlying mechanisms of octopus arm behaviors and testing existing models of the arm. On the one hand, tasks can be designed to encourage behaviors such as search, manipulation, and locomotion, from which mechanisms can be isolated and programmed into models subjected to a simulated task in order to compare results. Alternatively, arm models can be provided with a task to predict what the octopus arm will do in a given situation, which can then be validated with a 3D printed version of the task presented to an octopus. This will be particularly useful as more sophisticated models are developed with multisensory capabilities and more accurate morphological and biomechanical properties. The fact that these tasks are printed from CAD files means that, provided printer settings are identical, the exact same task can be printed in multiple locations and used for multiple species, ensuring optimal replicability. This will necessarily be subject to slight differences in resolution depending on the capacity of the printers.

Sucker recruitment presents a simple peripheral behavioral mechanism that can lead to a number of adaptive advantages. By orienting suckers toward relevant stimuli, recruitment signals can act as an effective capture strategy. Multiple suckers can be recruited in immobilizing and handling prey where a single sucker may be insufficient. Given the minimal bandwidth between the brain and arms and the level of abstraction of mechanical information from the sucker disks (Wells & Wells, 1957), it seems like any one sucker’s ability to communicate with the brain is limited. By recruiting their neighbors toward a relevant stimulus, the representation of a stimulus within the brain can be compounded through the collective sensory fields and afferent pathways of recruited suckers. Sucker recruitment can thereby serve as an adaptive, locally controlled sensory filter. Additionally, as supported by our results, sucker recruitment serves as an effective search strategy by allowing the arm to conform to the shape of surface features, and a mechanism by which the octopus can exploit these surface features as a means to shape its arms with minimal feedback to the brain, and thereby confine the arms' degrees of freedom to a more tractable range.

Chapter 4. Octopus multi-arm search patterns over complex surfaces

4.1 Introduction

The octopus's arms are remarkably adaptive both mechanically and functionally. They can bend anywhere along their length in any direction, giving them effectively infinite degrees of freedom (Kennedy et al., 2020; Kier and Smith, 1985; Kier and Stella, 2007), and are employed in virtually all the octopus's most common behaviors, including locomotion, foraging, exploration, excavation, and manipulation (Packard et al., 1988; Mather, 1998; Hochner, 2008). The octopus arm therefore presents an exciting biological inspiration for soft robotics. As the biomechanical and computational properties of the arm are uncovered, these properties can be implemented in the development of a soft robotic limb with the same range of capabilities.

Suckers stagger down the length of each arm as a chain on the ventral (bottom-facing) side typically in the hundreds (Young, 1965; Gutfreund et al., 2006). Most of the octopus's nervous system exists as a nerve cord extending down the center of each arm (Young, 1963; Rowell, 1966; Budelmann and Young, 1985). Within the nerve cord, localized motor pathways coordinate behavior while integrating chemotactile information from the suckers. Between the brain and nerve cords, there is a significant reduction in bandwidth. It is estimated that the brain and optical lobes, with around 170 million neurons, communicate with the arms and suckers, with around 360 million neurons, through a pathway of about 172 thousand axons (Young, 1965; Matzner et al., 2000; Rokni and Hochner, 2002; Nesher et al., 2019). Much of the information within the arms and suckers is therefore heavily abstracted or lost entirely upon ascending to the brain. Proprioception, as a notable instance, seems to be shared within and between arms, but has no representation within the brain (Wells and Wells, 1957; Wells, 1964; Rowell, 1966). The brain is therefore limited in its ability to send a detailed motor plan to the arms. Instead, it appears to send generalized motor plans which activate the locally organized motor pathways within the arms (Zullo et al., 2009; Zullo et al., 2019). Many of these pathways and their corresponding behaviors, including reaching, recoiling, as well as sucker adhesion, probing, and recruitment, remain largely intact even when the arm is separated from the brain (Rowell, 1963; Graziadei, 1965b; Rowell, 1966; Altman, 1968; Sumbre et al., 2001; Gutfreund et al., 2006; Zullo et al., 2011; Hague et al., 2013; Katz et al., 2021).

The octopus's arms have been described as highly independent, with arms appearing to execute separate motor patterns in parallel. This has been attributed to the degree of decentralization and autonomy of the arm's motor pathways (Mather, 1998). While multi-arm behavior and coordination has been a focus of a number of investigations (Buresch et al., 2022; Bidel et al., 2022; Byrne et al., 2006; Levy et al., 2015), few steps have been taken to isolate the arms within separate task spaces to minimize interaction and visual occlusion for recording.

Though sucker recruitment is among the behaviors that can operate with minimal feedback from the brain, it provides a remarkable range of advantages. Sucker recruitment occurs when suckers encounter a stimulus, such as a prey item, and neighboring suckers orient toward the source of this stimulus. These suckers may then recruit their neighbors as more and more suckers bend toward or conform around an object or feature that initiated the recruitment signal (Rowell, 1963; Altman, 1968; Gutfreund et al., 2006; Zullo et al., 2011). This serves as an effective mechanism for prey capture, for locally evaluating the salience of sensory input, for simplifying arm control (by exploiting surface shape to limit the arms' degrees of freedom), and for conforming around environmental features during foraging and exploration (see Chapters 2 & 3).

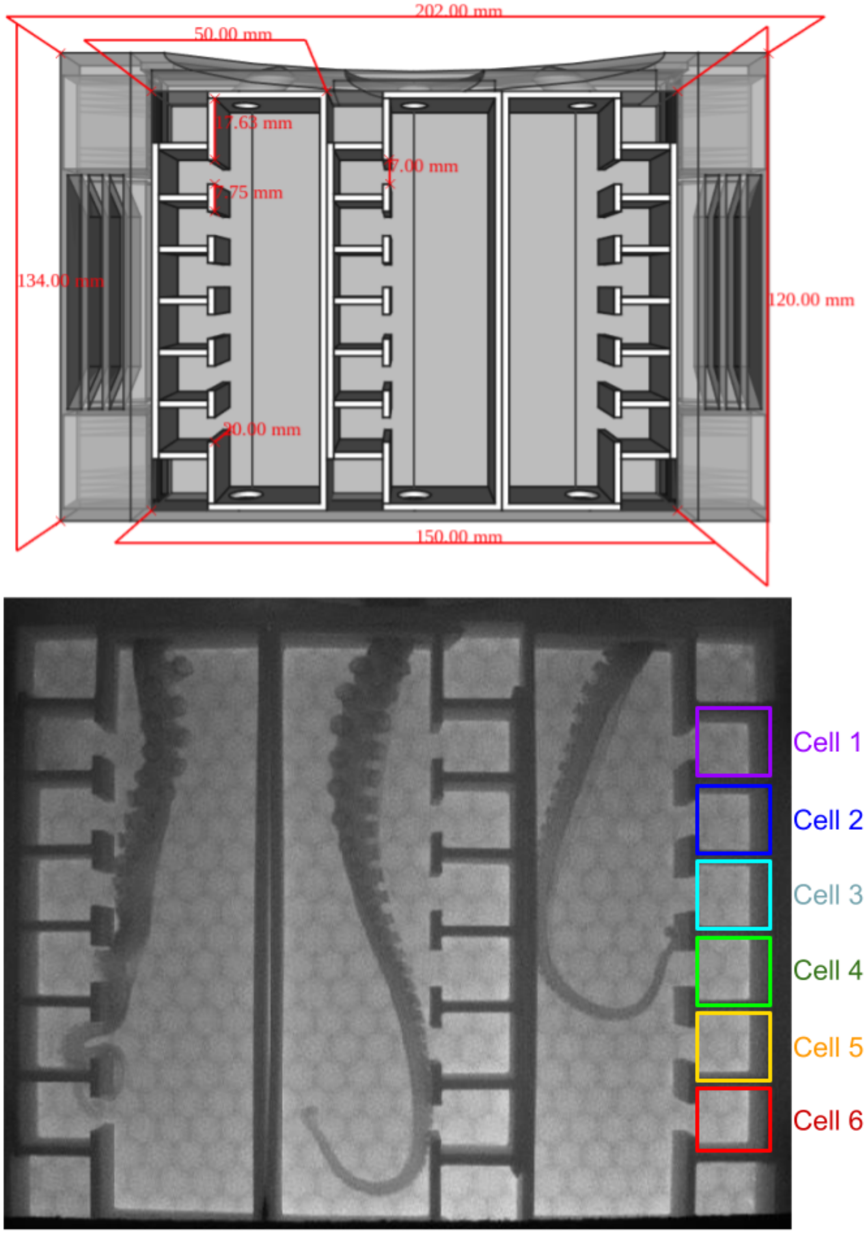

Figure 4.1. FreeCAD design of the task spaces and frame from a trial recording. Cells were assigned numbers 1-6 based on distance from the entrance.

Beyond the geometrically simple arm tasks used in laboratory settings, exactly how the octopus employs recruitment-led surface conformation when searching over the complex, convoluted surfaces of its natural habitat has not been well-studied. The focus of this investigation was therefore to identify the search patterns employed by the arms within a convoluted task space, which included a row of six regularly spaced openings leading to smaller subsections. Three of these task spaces were arranged in parallel to characterize similarities between multiple arms foraging at once.

4.2 Methods

Subjects for this study included four male Pacific red octopuses (*Octopus rubescens*) and one female giant Pacific octopus (*Enteroctopus dofleini*), which were collected under an approved permit through the Washington Department of Fish and Wildlife. Subjects were housed in separate tanks and were transferred to an experimental tank for training and trials. They were enriched and handled regularly during the course of the experiment. All experiments were carried out in accordance with a protocol approved by the University of Washington Institutional Animal Care and Use Committee (IACUC).

The task was designed in FreeCAD and 3D printed with white polylactic acid (PLA) filament. The task was secured against the side of the tank using magnets such that the interior task space was visible to a camera outside the tank but not to the octopus. The task interior was shaped as an empty narrow box with three parallel entrances at the top. Different variations of the task space could therefore be inserted into the interior.

Subjects were trained to reach into the task by leaving food on the top of the task. Once they readily approached and reached into the task, a training task space was placed inside. This was small, where the reward was easily within reach. Once the subjects readily approached and reached into the task, the training task space was replaced by the experimental version and trials began. Each subject was given as many opportunities as they needed to find at least one of the food rewards 12 times, with a trial considered the time searching leading up to a success and 60 seconds following.

Each task space contained one large rectangular section with one flat side and one side with six evenly spaced openings leading to separate square subsections (cell) in a row. Rewards were assigned to a combination of task spaces and cells based on a pseudorandom pattern. If multiple task spaces contained a reward, the reward was hidden within the same cell number. For the first six trials, two to three of the task spaces contained a reward and for the last six trials, only one of the task spaces contained a reward. The cells for the left task space were on the left side from the camera's view, cells for the right task space were on the right, and the middle task space alternated.

Arm behavior during trials was recorded with a CMOS camera (Imaging Source, model DMK 37BUX287) at 250 FPS, and videos were downsampled to 25 FPS for analysis. The arms were tracked using background subtraction and task cells were segmented both with automated Python routines. A number of metrics were used to characterize search patterns. Arm size was calculated as the number of pixels of the arm outline. Arm reach was calculated as the farthest distance into the task space occupied by the arm. Arm curvature was defined as the Kolmogorov-Smirnov (K-S) statistic comparing the distribution of the skeletonized arm outline to a straight line projecting from the task space entrance, with each set of pixel values representing distance from the task space entrance. Surface conformation was defined as the amount of overlap between the arm and a single pixel-width outline of the task interior as a proportion of the arm’s size. Cell occupancy was calculated based on the size of the arm in each cell.

4.3 Results

To broadly characterize the arms’ search pattern, a time lagged cross correlation related arm reach, arm curvature, surface conformation, and cell occupancy for all trials and subjects. For each trial this generated a series of distributions of Pearson’s correlation coefficient reflecting the synchrony of arm reach and the other metrics over a range of lagged time intervals. These distributions were then averaged across trials producing Figure 4.2a. This shows a general profile of the arms’ search pattern for 20 seconds leading up to and following occurrences of arm reach. Reaching is shown to be closely aligned with distal cell occupancy and followed by proximal cell occupancy, with more proximal cells having a longer occupancy time. Curvature and surface conformation lag behind reaching along with proximal cell occupancy, showing that while distal cells are occupied with an outstretched arm, the arm is not conforming to the shape of the cells in this state. As the arm progresses proximally, it shows greater curvature and greater degree of conformation to cells.

To characterize patterns of cell occupancy, a sequence was generated for each trial based on the most recently occupied cell. From these sequences a transition matrix was created, which is shown diagrammatically in Figure 3b. These results showed a stronger preference for a distal-to-proximal than for proximal-to-distal search pattern, with proximal cells instead showing a greater probability of reentry. There was a greater probability of skipping cells during distal-to-proximal search.

To assess the degree of arm independence, the Pearson correlation coefficient was calculated for arm size, reach, curvature, and surface conformation from all occurrences of arms

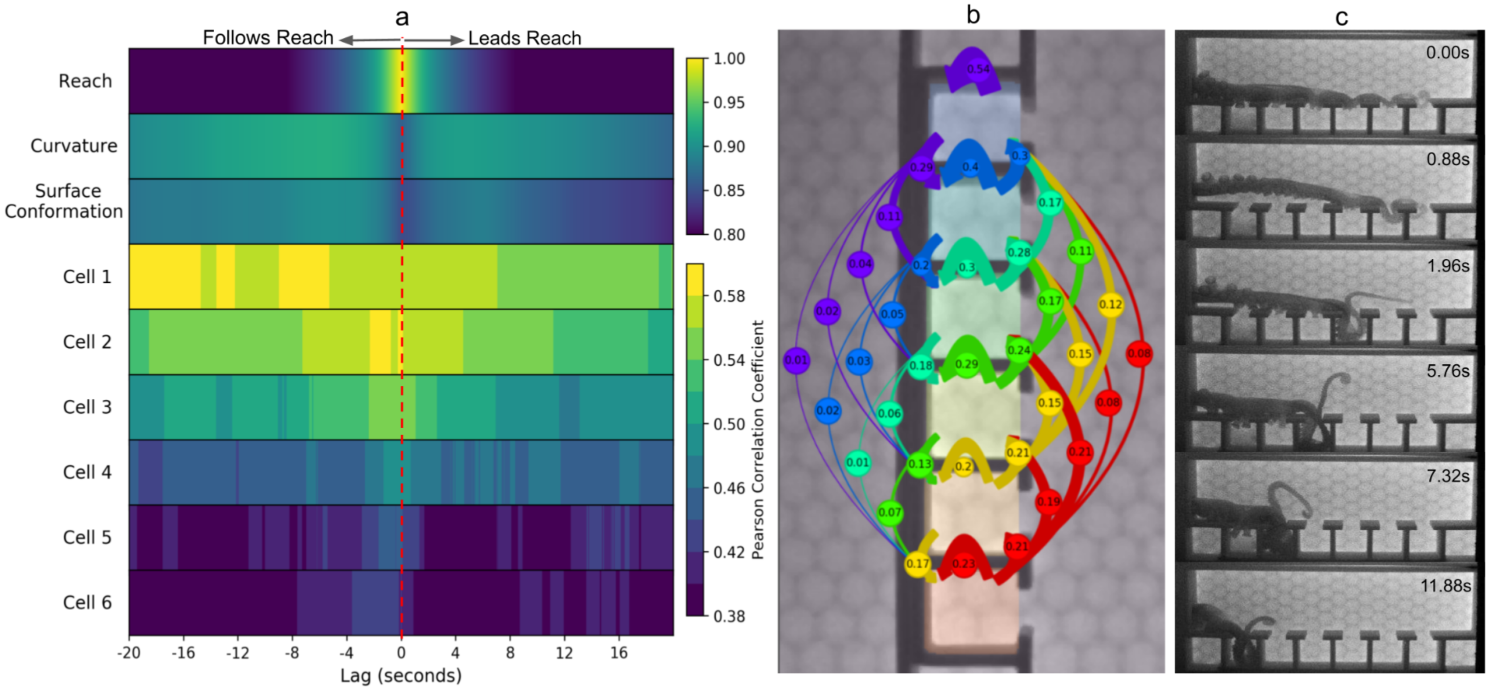

Figure 4.2. (a) Average time lagged cross-correlation of all trials showing occurrences of arm curvature, arm surface conformation, and cell occupancy and how they correlate with occurrences of arm reaching (at Lag = 0) 20 seconds ahead of reaching (right of plot) and 20 seconds following reaching (left of plot). (b) Transition probability diagram showing the probability of the arm's most recently occupied cell given its previously occupied cell. (c) Example of an arm performing a systematic distal to proximal search pattern.

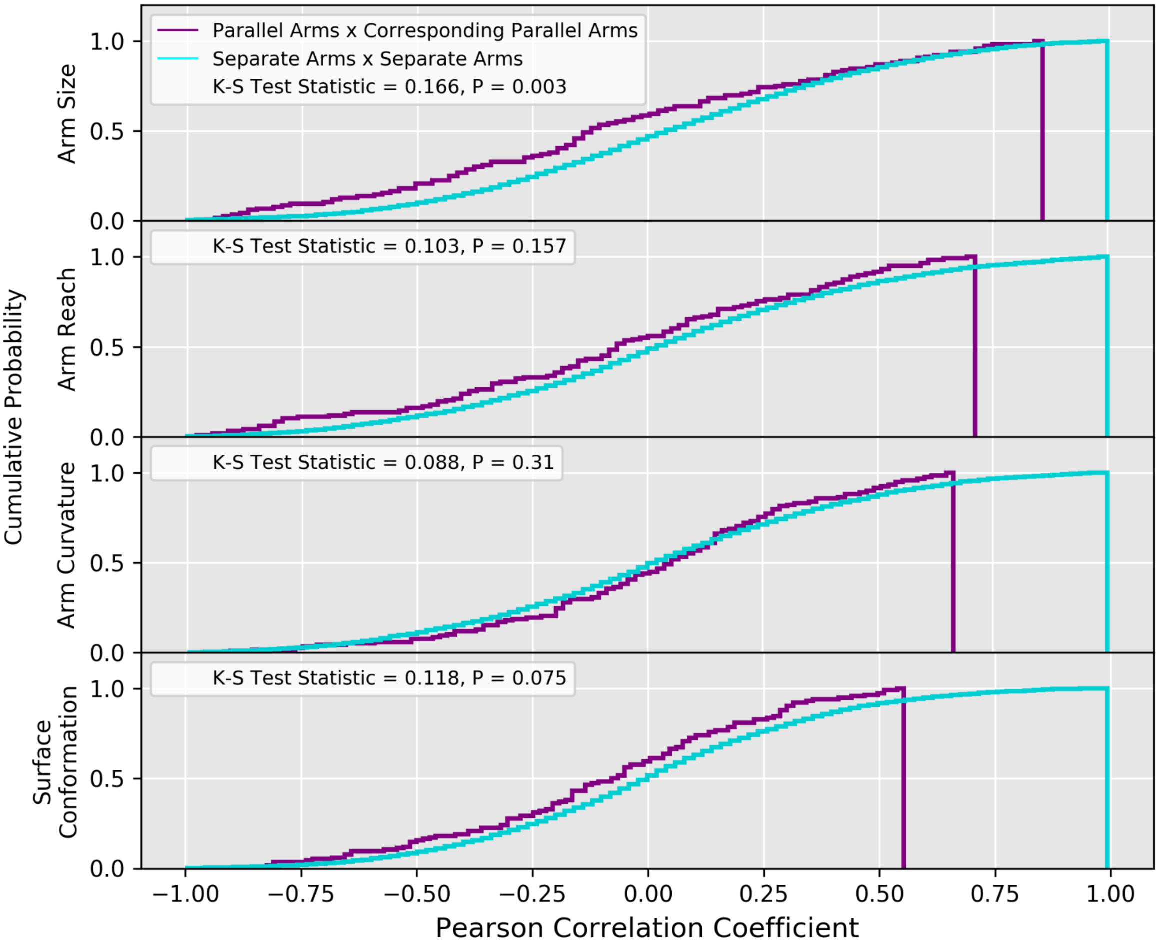

Figure 4.3. Cumulative probability distributions of Pearson correlation coefficients comparing arms foraging in parallel with their corresponding parallel arm and comparing arms foraging separately. These distributions were compared with a K-S test. Arm size among parallel arms was significantly more likely to be anticorrelated, while no significant difference emerged among the other metrics.

foraging simultaneously in separate task spaces (parallel), and for all occurrences of arms foraging separately. The two distributions were therefore created for each metric, one representing the correlation profile of parallel arms and other representing that of separate arms. A K-S test was then used to compare the two distributions for each metric. Results are shown in Figure 4.3. Distributions of arm reach, curvature, and surface conformation showed no significant difference, while the distribution of parallel arms were significantly more likely to be anticorrelated. Overall these results suggest that for reach, curvature and surface conformation, arms searching in parallel are not more likely to be correlated or anticorrelated than arms foraging separately, while it is more likely for parallel arms to alternate in the how much of each arm is searching their respective task space.

4.4 Discussion

While recruitment-led search patterns over simple surfaces would seem to follow a predictable pattern of conforming to the surface shape with a particular preference for concave edges (see Chapter 3), in its natural environment the octopus would encounter a variety of complex surfaces, including crevices of various shapes, sizes and regularities. Hidden among these surfaces are prey which the octopus is able to locate and extract using just its arms and suckers. How does the octopus adapt its search strategy to successfully forage over these surfaces? Our results reveal a possible method.

The three task spaces in this study included a row of openings into cells, and within one of these cells a food reward was hidden. Complete conformation to the task space surface, which may be a successful strategy in task spaces with simpler geometries, would have been unlikely to lead to a successful trial if the arm was not long enough to follow the outline of the task to the reward location, particularly when found in distal cells. It was therefore common for the arm to extend across all openings with its suckers probing into the gaps in the surface, then search in a single cell to a few cells at a time. Where the arm entered the cell appeared to be a recruitment-led conformation, but only within a section of the arm. Therefore, when encountering multiple openings in a surface, the arm can isolate recruitment to specific sections to explore into a single opening, rather than needing to conform against the entire surface at once.

The results from the time lagged cross correlation and transition matrix revealed a general search pattern including the order that cells were occupied. When outstretched, the arm explores distal openings then works its way proximally as the arm as it shows greater curvature and surface conformation. Optimizing surface conformation for proximal openings makes sense as using this strategy in openings easily within reach would not limit the arm's ability to reach more distal openings. While cells were commonly skipped, particularly in the proximal direction, the most likely transition for cells 2-5 apart from reentry was to the immediately proximal cell. Figure 4.3c shows an example of an arm serially searching through cells 5-1.

From these results we propose the following mechanism. When outstretched along a surface, the suckers encounter and signal the location of irregularities, which in this case are openings in the surface. A mechanism–which could reasonably occur in either the arm or the brain–then prioritizes these openings and sends an inhibitory signal to the arm section distal of the opening of highest salience while localized recruitment conforms the now free arm section into the opening. In the case of equally salient openings, priority defaults to the distal-most opening. Then, once explored, this process is repeated for the next opening. This allows the arm to perform a systematic search of all encountered openings by simply alternating between distal inhibition and recruitment.

Realistically, salience would never be truly equal at multiple points along the arm. Chemical cues, fluid motion, and the size and configuration of the arm and suckers are all likely factored into salience evaluation. This is likely the source of cells being skipped or taking immediate precedence. Interestingly, the arm commonly performed a systematic search even with the presence of an attractive chemical indicating the presence of food within a proximal cell (see Figure 4.3c). If the suckers are relaying the presence of food, this behavior may suggest that the octopus chooses to perform the entire search pattern rather than prioritizing proximal cells, possibly because these cells fall along an intended search path. This behavior further suggests the presence of an exploration-exploitation balance that may be affected by satiation levels and predation threat.

The narrow architecture of the present task space limits lateral motion in the arm, so while the search mechanism proposed here would be effective in narrow spaces, it fails to account for lateral search over wider surfaces. However, results from Chapter 3 show a preference for the arm to search along concave edges. These results therefore suggest that the arm preferentially searches along surface contours, then proceeds to search through smaller openings along the contour using the mechanism described here.

The degree of arm independence during the task was assessed by creating a distribution of Pearson correlation coefficients comparing arm size, reach, curvature, and surface conformation between arms foraging in parallel and between arms foraging separately, and comparing these distributions using a K-S test. Our results show that reach, curvature and surface conformation among arms foraging in parallel are not significantly more or less correlated than arms foraging separately. However, parallel arms are more likely to be anticorrelated in size compared to separate arms. This likely reflects a feature of the task itself. The closer the octopus is to any one of the entrances, the more of its arm it can reach into the corresponding task space, but this limits the size of the arm it can reach into the other task spaces. Unfortunately, arms cannot be easily identified using the methods employed in this study, so we cannot assess whether varying patterns emerge when comparing neighboring arms foraging in parallel to non-neighboring arms foraging in parallel.

Our findings highlight the advantages of limitless degrees of freedom. By employing a simple behavioral program in its arms combining sucker recruitment with distal inhibition, the octopus can perform a systematic search pattern over even the most complex surfaces.

Chapter 5. A 3D printed octopus-inspired soft robotic arm

5.1 Introduction

In the context of robotics, movement can be understood as the reconfiguration of joints to reposition an effector in space. An effector is a device used to interact with the environment. In biology this could be considered a number of appendages, such as a foot, hand, antennae, jaw, tongue, or claw. The configuration space represents all of the possible combinations of joint configurations available to reposition this effector. The degrees of freedom of each joint are represented by a dimension or axis of this space. An effector connected to a simple revolute or hinge joint could be represented by a configuration space of a one-dimensional axis. Typically, as the number of dimensions increases, so does the number of possible paths through this space representing the combination and order of joint adjustments between any two configurations. In biology, these paths through the configuration space are determined by balancing a number of factors, and are typically optimized for speed, energy conservation, or computational simplicity.

Traditionally rigid robotics takes a great deal of inspiration from skeletal animals such as vertebrates and arthropods (Floreano et al., 2009; Zhou & Bi, 2012; Wright et al., 2007; Unver et al., 2006; Kovac et al., 2008), whose configuration space is confined to a manageable number of joints with relatively few degrees of freedom. In the field of soft robotics, on the other hand, we are faced with a far greater range of configurations and are limited in the extent to which we can translate traditional principles of robotic control (see Chapter 1). Conveniently, soft bodied control is performed by the octopus in virtually all aspects of its life. Not only does the octopus employ control strategies capable of coordinating the infinite degrees of freedom of its arms across a wide range of behaviors, these behaviors gain a number of advantages from this extreme mechanical flexibility (see Chapters 2-4). The octopus therefore serves as an ideal model for soft robotics as it not only successfully controls limbs with infinite degrees of freedom, but prevalently exploits this property to generate adaptive behavior.

In a few cases, the octopus arm executes patterns of muscle activation that are largely conserved or "stereotypical," as seen in reaching and fetching behavior. Reaching behavior is characterized by a wave of muscle contraction down the length of the arm, which resembles a propagating bend in the direction of a target. The direction in which this extension program is directed is likely determined by the vertical and horizontal angle of the arm prior to activation (Gutfreund et al., 1998; Sumbre et al., 2001; Gutnick et al., 2020). This results in a feedforward pattern of activation that is not modified once initiated. Meanwhile, fetching occurs when an object along the arm elicits the activation of two converging signals of muscle activation from its location in the proximal direction and from the base of the arm in the distal direction. Where these signals meet determines where the arm will bend to pass the object to the mouth (Sumbre et al., 2006).

In other cases, sucker recruitment causes the arm to conform to the shape of objects and surfaces in the environment. This has the effect of confining and simplifying the arms' range of configurations as well as capturing and handling prey, searching over complex surfaces, and evaluating the salience of sensory input (Chapters 2-4).

In all of these behaviors, mechanisms are employed to reduce the dimensionality of the arms' configurations. Though the configuration space of the octopus's arms is extremely large, reaching, fetching, and surface conformation follow computationally conservative pathways through this space that guide the arms from one configuration to another.

It is important to note that for these behaviors, no particular sucker or arm section is functionally unique or vital. Reaching and surface conformation appear to employ identical routines within each unit of sucker and its adjacent section of arm, and the same seems to be true for fetching as the pattern of bending is only dependent on the location of the object of interest and can be activated anywhere along the arm.

Morphologically, sucker-arm units including the nerve cord appear to be segmented down the arm, but the extent to which this is true has not been characterized. We can say, however, that the arms show strong evidence of being functionally or “algorithmically” segmented in that each sucker-arm unit may be following identical routines from which a number of arm behaviors are generated. Therefore, what seems to be the octopus’s approach to the problem of dimensionality is to perfect a single unit mechanically and computationally and assemble multiple units end-to-end. We therefore also adopted this approach for the design and development of a soft robotic arm, and describe our methods here. The prevalence of recruitment, both as a control strategy and in its key role in a number of behaviors, posed it as a useful initial behavior. If properly implemented, this behavior could likely provide the same functional and computational benefit for the robotic arm.

5.2 Methods

The robotic arm segment consisted of four pneumatically controlled soft actuators and a soft gripper that likewise served as a contact sensor. These elements were assembled as a single segment and connected to the neighboring segments by a rigid clover-shaped adaptor of four

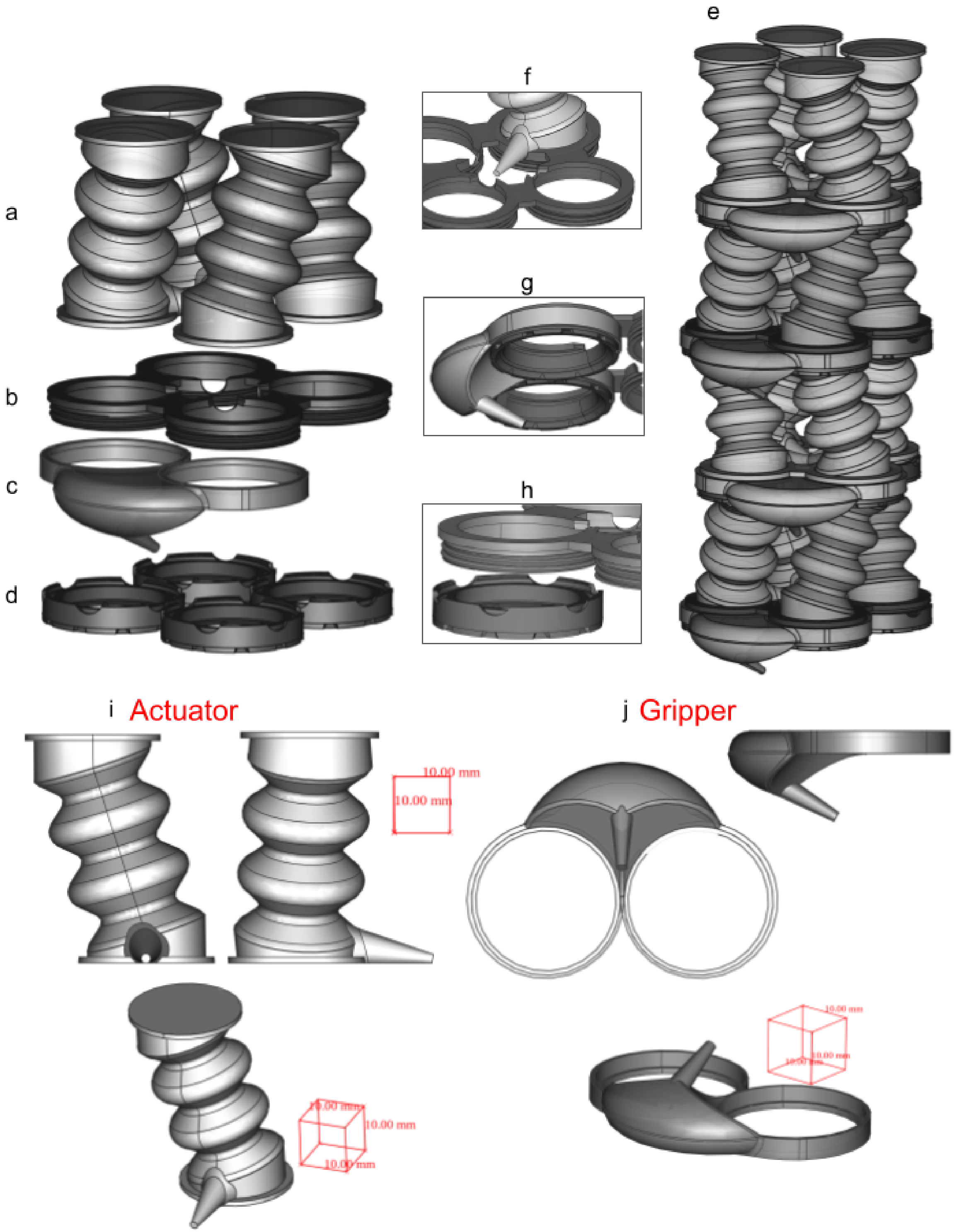

Figure 5.1. Robotic arm components. (a-d) Components of a single segment: (a) set of four actuators (b) clover-shaped adaptor with four connected male-threaded rings (c) gripper (d) set of four female-threaded rings. (e) Four assembled segments. (f) Placement of an actuator in the adaptor. (g) Placement of the gripper secured around two adaptor ring sets. (h) Close-up of threaded adaptor components. (i) Actuator and (j) gripper.

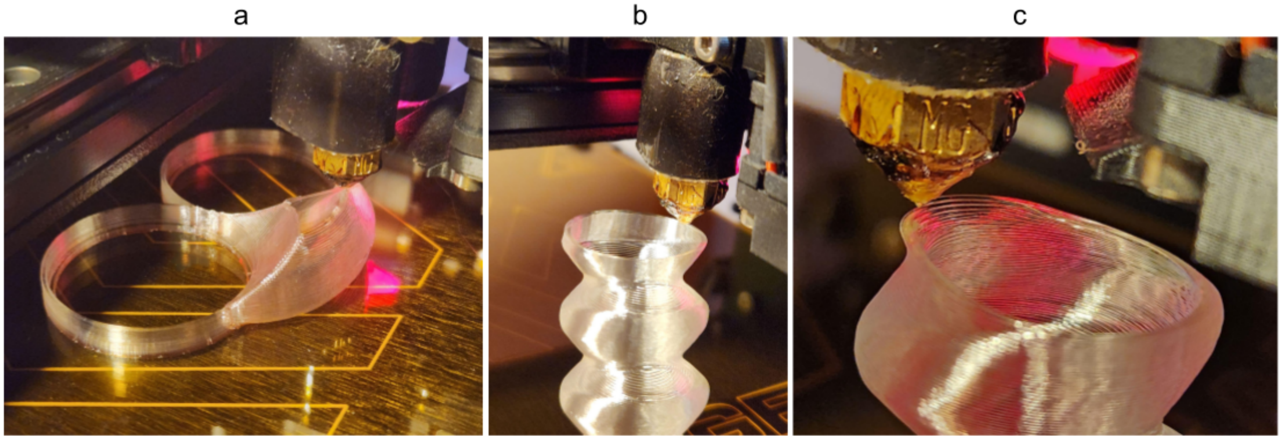

Figure 5.2. Vase mode printing of the (a) gripper and (b & c) actuator.

male-threaded rings and four female-threaded rings. The actuators were accordion shaped and oriented diagonally, alternating in their orientation for each segment. This gave the arm a capacity for rotational movement and alternated the orientation of the gripper in a similar pattern to the suckers along the octopus's arm, this was meant to provide an indication of the direction of a stimulus. Each actuator included a flat rim on both ends which were tightened between the adaptor rings. The gripper was secured to the segment assembly by two rings that each wrapped around a ring of the adaptor. These two rings also included a rim that was likewise secured between the adaptor rings. All of these components were designed with FreeCAD, prepared for printing with Simplify3D and 3D printed with a Makergear M3-ID.

The actuators and gripper were printed from Ninjaflex (polyurethane thermoplastic) filament using the vase mode settings in Simplify3D. Vase mode is common among 3D printer slicing software, and prints only the outline of the file in a single, constant spiral. With consideration given to the surface gradient in designing the CAD file and to the relevant printer settings, vase mode in combination with Ninjaflex can print soft, tight sealing bladders in a wide variety of shapes. This also made for very light components overall and conserved material. The adaptors were printed with polylactic acid (PLA) filament.

The variable settings feature of Simplify3D was used to assign separate non-vase settings to the initial layers of the gripper and flat top and bottom of the actuators, as extra rigidity was needed for these areas and because vase mode can easily fail on flat, horizontal surfaces without a supporting structure.

The actuators and gripper included an elongated cone-shaped projection that served as a connection point for pneumatic tubing. Because this feature was likewise printed in vase mode, its tip needed to be cut after printing. From here, each actuator was connected to a vacuum pump

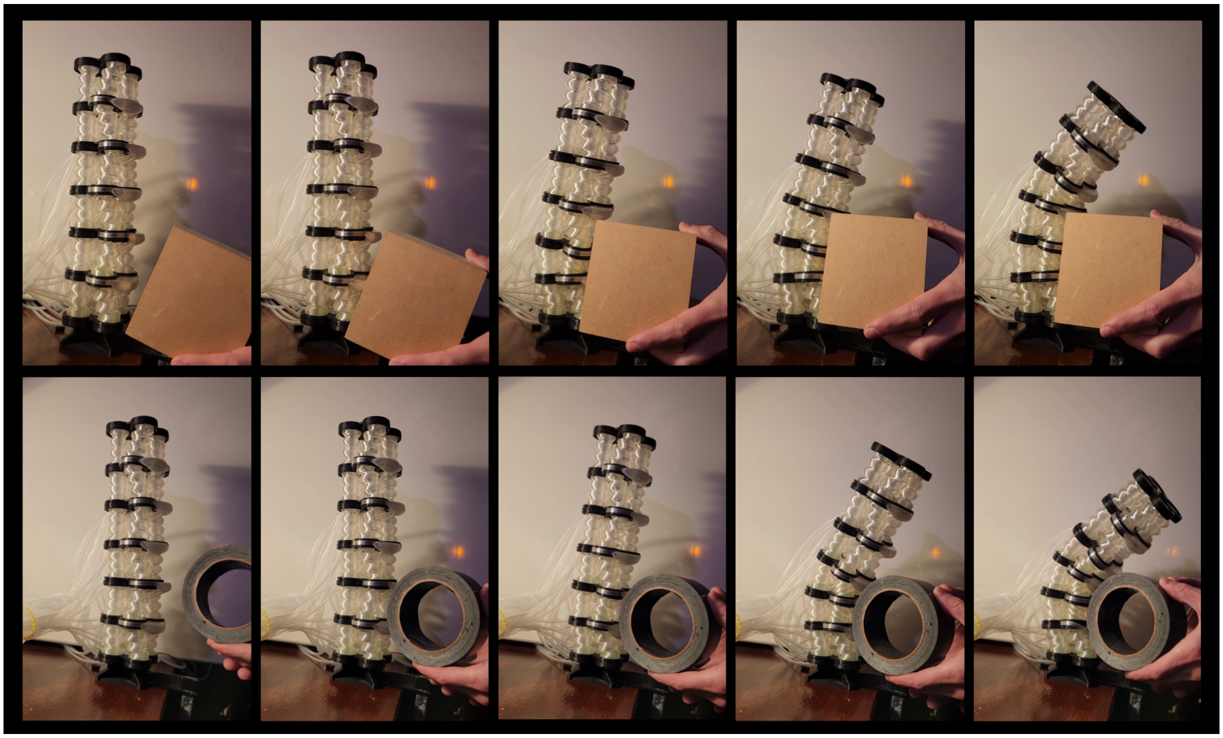

Figure 5.3. Recruitment performed by the robotic arm initiated by contact with two differently shaped objects.

by an air valve, all through silicone tubing. These air valves were triggered by an Arduino through a relay which allowed for the control of individual actuators.

The air pressure inside each gripper was monitored by a connected pressure sensor wired to the Arduino. This pressure would fluctuate when the gripper came into contact with an object or surface. When the gripper pressure reached a threshold, the closest pair of actuators on the neighboring segments activated, causing neighboring grippers to bend toward the site of contact. If these grippers were likewise triggered, they activated the next segments and so on, mimicking a wave of sucker recruitment in the octopus arm.

The important printer settings used for the vase mode layers of the actuators and grippers are shown in Table 4.1. These settings were chosen with the need to balance a number of key factors. If layers were too short, prominent warping occurred, especially in areas with finer surface features. This warping caused the extruder to easily “derail” from the previous layer. Meanwhile, if layers were too high, abrupt horizontal shifts between layers on gradients caused gaps to appear. If the extrusion width was too thin, walls were often weak (particularly surfaces of shallower gradient), and more susceptible to leaks. If extrusion width was too thick, the print would be stiffer, resulting in a less responsive gripper and requiring a stronger vacuum for actuation.

5.3 Discussion

Biology provides an endless source of inspiration for technological innovation and robotics in particular has massively benefited from implementing the mechanical properties of living organisms. Given the ubiquity of non-rigid materials among these organisms, soft robotics especially has much to gain from understanding the varieties of morphological properties and control strategies employed in the biological world. As potential alternatives to traditionally rigid robots, soft robots are lightweight, low-volume, and flexible. With the octopus arm able to maneuver over uneven terrain, navigate and explore confined spaces and complex surfaces, grasp and manipulate objects of virtually any shape, and operate autonomously with little feedback from a centralized controller, implementing the biomechanical and computational properties of the octopus arm in the development of a soft robot could lead to a great number of applications. This kind of versatile robot could benefit manufacturing, assembly, surgery, prosthetics, search and rescue, underwater search and recovery, and exploration.

What stands out among the octopus's biomechanical and computational adaptations is how prominently they serve the octopus's exploration and searching behavior. Whether in finding prey, places to hide, or passage through an obstacle, the octopus's arms are uniquely qualified. The most promising applications of an octopus-inspired robot are therefore in facing analogous challenges. Deep sea and planetary exploration, as well as search and rescue, and search and recovery pose particularly useful avenues for implementing these adaptations.

The design presented here has potential for a great number of improvements that can be explored and we will discuss only a select few of them here. The use of 3D printing makes for straightforward manufacturing and minimizes the need for human involvement. However, this design lacks a means for autonomous assembly and requires rigid parts to join each segment. Both of these problems can be solved with a segment that can entirely be generated and serially joined in one print. This could also allow for easily resizing the arm depending on the application. However, this could potentially compromise many of the benefits gained from vase mode, which relies on a single pass for each layer. For use in water, the pneumatic system employed here can be replaced with a hydraulic system. Multiple arms may also be connected at a midpoint, providing a number of advantages of the octopus’s multiple arms, such as locomotion, manipulation, and search/exploratory radius. There are also a wide variety of alternative materials that could be used depending on the application and environmental conditions. Cheaper and more widely available materials, software, electronics, pneumatic hardware, and 3D printers may be used as alternatives to what was used here, thereby allowing for a greater number of people to benefit from and contribute to this technology.

Table 5.1. Printer settings for actuator & gripper vase mode layers

Nozzle diameter	0.75mm
Extrusion multiplier	1.20
Extrusion width	Actuator: 0.90mm; gripper: 0.80mm
Layer height	0.22mm
Vase mode	ON
Infill	0%
Supports	OFF
Extruder temperature	250℃
Bed temperature	OFF
Cooling fan speed	100%
Printing speed	10mm/s

Chapter 6. General Conclusions

With its arms able to bend anywhere along their length in any direction, the octopus's space of possible configurations is immeasurably large. Despite the control problem that this would seem to present, the octopus's flexibility poses no challenge to it. Rather, this flexibility serves as a mechanical property that the octopus exploits across a variety of behaviors. Most prominently, through sucker recruitment, a mechanism localized with the arms, this flexibility allows the arms to conform to surfaces in the environment. By doing this, the octopus brain delegates the decision of arm shape to the arms themselves and the chemical and mechanical makeup of the environment as conveyed by the suckers. Surface conformation serves to confine the arms' degrees of freedom. Instead of needing to choose one of an infinite combination of muscle adjustments to reshape its arm, the surface acts as low dimensional reference, guiding the octopus and its arms along a predefined path through their vast configuration space much like how a ship at sea may use coastlines for navigation. If instead the octopus's goal is to capture a visual target or pass an object proximally, the arms adopt a stereotypic pattern of muscle activation–separate but similarly direct and reliable paths through the configuration space. Beyond its operational and computational significance, recruitment contributes to prey capture, systematic search patterns over complex surfaces, grabbing and manipulating objects of any shape, and evaluating the salience of sensory input. This poses recruitment not just as a relevant behavior worth pursuing in the development of soft robotics, but as a vital mechanism of soft-bodied control.

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