

# New Insights on the Control and Function of Octopus Suckers

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Octopuses utilize their suckers for a myriad of functions such as chemo- and mechanosensing, exploring and manipulating objects, anchoring the body during crawling, and navigating through narrow passages. The sucker attachment mechanism grants the octopus the ability to perform many of these tasks. The goal of this study is to analyze sucker function and control through the assessment of pull-off forces under different conditions. Sucker pull-off forces are measured in *Octopus bimaculoides* (three females, seven males), when the arm is intact, amputated, and amputated with the suckers punctured. Greater sucker pull-off forces are observed for amputated arms, plausibly indicating that the brain and/or the interbranchial commissure are responsible for triggering early sucker detachment in the intact animal. In addition, after piercing and compromising the sucker cavity, pull-off force significantly decreases, indicating that the primary mechanism for sucker attachment is suction, and is less dependent on adhesion. These results provide new insights into the control and function of octopus suckers that can be integrated into the design and development of soft robot arms for aquatic applications.

unpredictable, unstructured, and confined environments.<sup>[1–8]</sup> However, despite recent advances in soft robotic technologies, the challenge of controlling high-dimensional appendages has prevented the development of versatile soft robots. Biology serves as a rich source of design inspiration for soft robots, which have been based on such diverse organisms as octopuses,<sup>[9]</sup> caterpillars,<sup>[10]</sup> snakes,<sup>[11,12]</sup> fish,<sup>[13]</sup> worms,<sup>[14–16]</sup> and humans.<sup>[17]</sup> Through the integration of biology, engineering, and physics, this study aims to investigate octopus control architecture in addition to sucker attachment and detachment mechanisms.

The octopus has a soft body and arms (Figure 1), and can achieve a diverse array of locomotor modes such as swimming, jetting, crawling, and even bipedal walking.<sup>[18]</sup> In addition, octopuses are capable of complex tasks such as carrying and manipulating objects and squeezing through tight spaces. Previous studies<sup>[19–23]</sup> have shown that octopuses use a stereotypical motion for grasping objects. Impressively, the same pattern has been observed in amputated octopus arms,<sup>[20,21]</sup> implying the presence of a distributed


## 1. Introduction

The ability to bend, deform, configure, and adapt to surroundings makes soft robots an ideal choice for navigating

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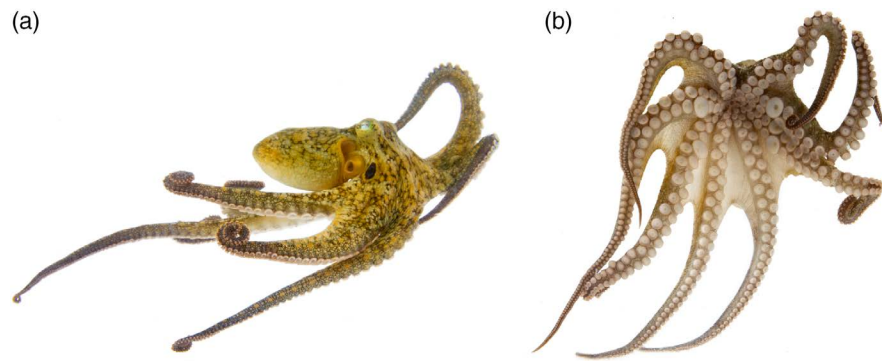
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**Figure 1.** *Octopus bimaculoides*: a) side view and b) oral view.

control architecture. The adaptability, limitless degrees of freedom, and distributed control of octopus arms make them an ideal candidate for inspiration in the areas of soft robotics<sup>[2,9,24–33]</sup> and control of high-dimensional systems.<sup>[4,34–41]</sup>

The octopus features an extensive nervous system, including the brain, an axial nerve cord in each arm, and the interbrachial commissure, a ring-like structure connecting all of the axial nerve cords.<sup>[42,43]</sup> Within the arms, the central axial nerve cord is accompanied by four peripheral intramuscular nerve cords and nerves that are associated with each sucker.<sup>[42,44–47]</sup> This network of nerve fibers and ganglia is embedded in layers of muscle, including transverse, longitudinal, oblique, and circular fibers,<sup>[48]</sup> granting the animal the ability to elongate, shorten, bend, and twist anywhere along the arm with high precision. Extraordinarily, the suckers display similar capabilities. The meridional, circular, and radial muscles<sup>[49,50]</sup> controlled by the sucker ganglia achieve a wide array of motor and proprioceptive functions. Octopuses also use their suckers for sensing and exploring the environment.<sup>[49]</sup>

An octopus sucker consists of two regions, the infundibulum and acetabulum (**Figure 2**). The infundibulum is the exposed, pliable, dented face of the sucker that is circumscribed on its rim by a ridge.<sup>[51–53]</sup> The acetabulum is the more rigid, ellipsoidal cavity of the sucker, consisting of a domed roof featuring a fibrillar surface and smooth surrounding walls.<sup>[50,53]</sup> Throughout the years, many investigators have postulated about the attachment mechanism of octopus suckers.<sup>[49,52,54,55]</sup> The proposal by Tramacere et al.<sup>[50,53,56]</sup> is the most thorough to date. According to these authors, the attachment process begins with the infundibulum pressing and conforming to the surface, and the rim sealing the sucker and preventing water leakage. The acetabulum then begins contracting radially, decreasing the inner water pressure. The meridional muscles then contract until the acetabulum's fibrillar protuberance adheres to the orifice sidewalls, forming a toroidal water cavity. Lastly, the acetabulum's radial and meridional muscles relax as the sucker configuration remains passively fixed due to the friction between the protuberance and side walls and the pressure differential created by the toroidal water cavity. During detachment, the contraction of circular muscles in the infundibulum and acetabulum ruptures the seal between the sucker rim and the surface, and the contact between the fibrillar protuberance and the orifice

sidewalls. This causes the internal sucker pressure to equal that of the surrounding environment.

While sucker attachment and detachment mechanisms have been described in previous studies,<sup>[44,49,50,52,53,55–60]</sup> a number of questions remain. In particular, this study was designed to assess whether pull-off force is impacted when there is no communication with the brain or interbrachial commissure, and the degree to which suction versus adhesion contributes to sucker attachment. To analyze these conditions, the pull-off force was measured in intact arms, amputated arms, and amputated arms with punctured suckers. The intact versus amputated arm experiments may provide insights into how the sucker attachment mechanism is influenced by centralized versus distributed neural pathways. Unpunctured versus punctured suckers were analyzed in amputated arms to determine the degree to which the attachment mechanism is dependent on suction versus adhesion. In addition, all eight arms were tested to determine whether there are any functional differences based on arm identity (i.e., in anterior vs. posterior, or right vs. left arms). The obtained results can potentially shed light on the control and function of octopus suckers.

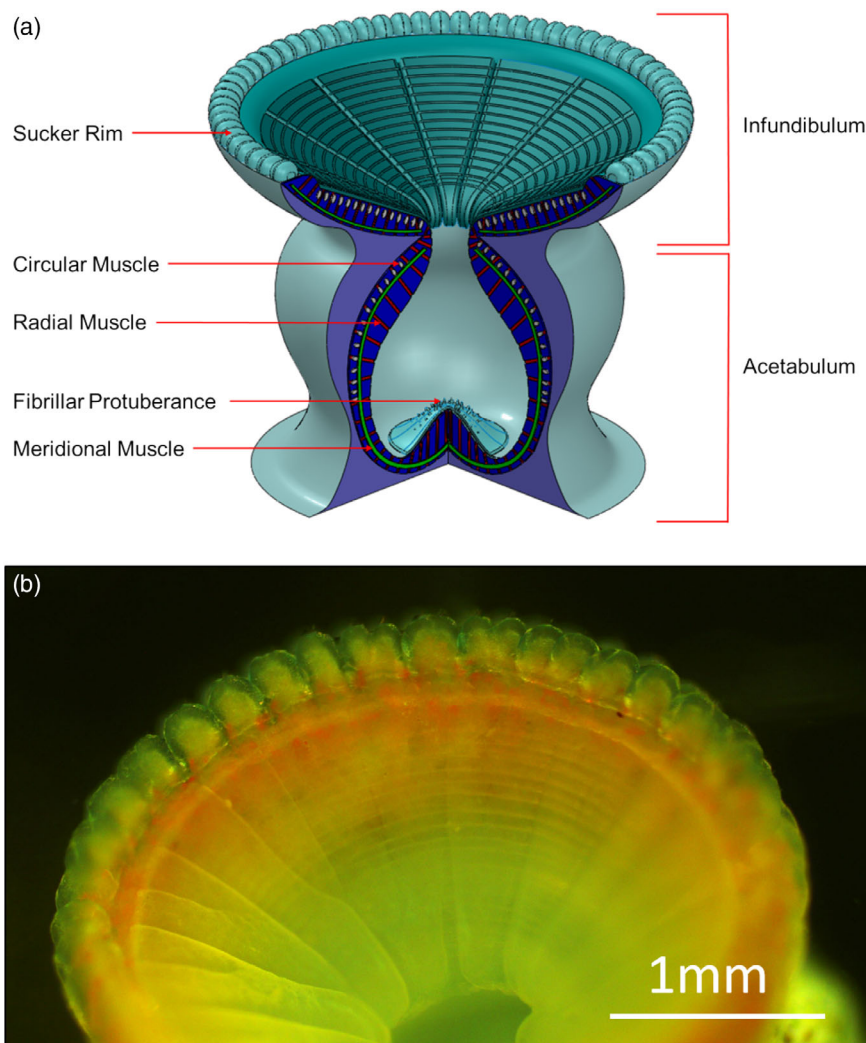
## 2. Experimental Section

### 2.1. Ethics Statement

Although Institutional Animal Care and Use Committee (IACUC) approval is currently not required for cephalopod research in the United States, the husbandry, anesthesia, and experimental protocols used in this study were developed under the supervision of Arizona State University (ASU) veterinary staff, referencing the EU Directive 2010/63/EU and published guidelines for cephalopod use.<sup>[61–68]</sup> The ASU IACUC reviewed a description of the proposed work and concluded that IACUC approval or waiver was not necessary. However, all protocols were developed in close collaboration with the ASU veterinary staff.

### 2.2. Animal Husbandry

Experiments were conducted on ten *Octopus bimaculoides* specimens (three females, seven males) with an average body mass of  $118 \pm 38$  g. This species is commonly referred to as



**Figure 2.** Octopus sucker: a) 3D sucker model with major regions and muscles labeled; b) 4× zoomed image of a sucker, highlighting the infundibulum.

the California two-spot octopus due to its distinctive ocelli. Animals were collected off the coast of southern California by Aquatic Research Consultants (San Pedro, CA) and shipped overnight to ASU, where they were housed in a vivarium in a large raceway at a temperature of  $17.8 \pm 0.1$  °C and water salinity (specific gravity) of 1.024–1.025 PSU. In the raceway, each octopus was housed in individual 30 L tanks containing a large PVC pipe for hiding and objects for enrichment (e.g., large Lego blocks). Animals were cared for by staff members of ASU's Department of Animal Care and Technologies and were fed a diet of live fiddler crabs, alternating with frozen shrimp, with a day of fasting in between. Sex was confirmed after the completion of experiments through dissection of the reproductive organs within the mantle cavity.

### 2.3. Anesthesia and Euthanasia Protocols

With the assistance and supervision of ASU's clinical veterinarian, the following anesthesia and euthanasia protocols were established. Animals were allowed to acclimate to the vivarium

for a minimum of 1 week prior to an anesthesia event. The animal was then transported from its 30 L housing tank to a 4 L experimental container with 1.5–2.5 L saltwater, depending on the animal's size. Ethanol (99% pure) was dispensed into the saltwater at 0.25% (4–5 mL) increments every 1–2 min until a maximum ethanol concentration of 1.4% was reached. Throughout the process, the animal's breathing cycle (i.e., mantle expansion and reaction) was monitored every 5–10 min to ensure a stable breathing rate. In addition, the animal was gently probed to assess responsiveness and determine the effectiveness of the anesthesia concentration. On average, it took  $14 \pm 1$  min to achieve anesthesia. After completing the intact arm experiments, described later, the arm was amputated and the animal was placed back in its housing tank where it recovered from the anesthesia within a matter of seconds. Animals were under anesthesia for an average of  $51 \pm 2$  min per experiment.

Typically, one arm was experimented upon per anesthesia protocol, with a 1 week gap prior to the next anesthesia event. However, the fourth and fifth arms were tested during the same anesthesia event. After completing experiments on the intact

fourth and fifth arms, both arms were amputated and the animal was euthanized. To achieve euthanasia, the ethanol concentration was increased to 10% in the experimental container, until the animal's breathing ceased. The remaining three arms were then amputated and preserved along with the mantle in 10% neutral buffered formalin for future anatomical studies.

## 2.4. Experimental Preparation

Once the animal was anesthetized, such that no active response was observed, the arm of interest was isolated. It should be noted that the order of the selected left (L) and right (R) arms varied per specimen to ensure data could be collected for all arm identities (i.e., L1–L4 and R1–R4). Arms were selected for study with consideration of the animal's mobility and ability to feed postamputation; this was achieved by alternating between anterior and posterior arms, and left and right sides of the animal over the course of the experiments.

The distal portion of the selected arm was anchored down to a small rectangular acrylic piece using superglue (Loctite® Super Glue ULTRA Liquid Control). As the arm was gently held and extended from the anchored distal end, a longer rectangular acrylic piece was positioned above the specimen, allowing the suckers to adhere to its surface. With the arm elongated and adhered to the acrylic, the skin on the aboral side of the arm was removed using fine scissors. A thin line of superglue was applied to another long rectangular acrylic piece, which was then situated under the arm, facing the deskinning aboral surface. With the arm now positioned between the two long rectangular acrylic pieces, it was held outside the saltwater until the aboral side adhered to the acrylic ( $\approx 1$ – $2$  min). Once the arm was adhered, the acrylic piece on the sucker side was gradually removed by disengaging the suckers. While arm stiffness does play an important role in the attachment and detachment of octopus suckers, further arm restraints were avoided to minimize arm and sucker muscle damage while maintaining the arm in a position that would enable replicable engagement of the suckers with the indenter. The potential effects of tissue stiffness variance were minimized through consistency in the experimental preparation and performing tests on the most proximal region of the arm in animals of similar size ( $p = 0.801$ ) (for more details on the statistical analysis, see Section 2.7).

A total of nine proximal suckers were selected and labeled using permanent markers on the acrylic piece next to the suckers of interest. Three neighboring suckers were designated for the intact arm, amputated arm, and amputated arm with punctured sucker experiments. Using double-sided tape (3M™ Ultra High Temperature Adhesive Transfer Tape 9082), the acrylic piece with the adhered arm was secured to the bottom of the experimental container with the suckers facing upward. At this stage the arm was ready for experimentation.

## 2.5. Experimental Setup

The test setup (Figure S1, Supporting Information) consisted of a 12 mm diameter borosilicate indenter with a radius of curvature of 37.22 mm attached to the end of a 102 mm long oxide alloy

steel screw, which was screwed into a 0.5 N (0.25 mN resolution) uniaxial load cell (Transducer Techniques® GSO-50) mounted onto a motorized linear translation stage (Thorlabs Z825V) with a 25 mm traveling distance (29 nm resolution). A 5 megapixel camera (EPL 170) was used for recording side view observations. Through a series of preliminary parameterization studies, optimal parameters were established for the indenter pull-off experiments (Appendix S1, Supporting Information).

## 2.6. Experimental Procedure

The 4 L experimental container holding the animal and adhered arm of interest was placed under the experimental setup. The indenter was lowered into the anesthetic (ethanol/saltwater) bath and zeroed out once centered above the sucker of interest. The sucker was approached by the indenter (velocity:  $0.2 \text{ mm s}^{-1}$ , acceleration:  $0.2 \text{ mm s}^{-2}$ ) and pressed upon until a preload of 7 mN was reached. The indenter remained in contact for 20 s and was then retracted (velocity:  $0.4 \text{ mm s}^{-1}$ , acceleration:  $0.2 \text{ mm s}^{-2}$ ) until sucker disengaged. One test per sucker was performed with the indenter cleaned (using an alcohol wipe) prior to each test.

Experiments were conducted on proximal suckers in 1) the intact arm, 2) the amputated arm, and 3) the amputated arm with the sucker sidewalls punctured. First, three designated intact arm suckers were tested for pull-off force. Once the intact arm sucker tests were complete, the arm was amputated with a scalpel and the animal was placed in its holding tank for anesthesia recovery, while the amputated arm was kept in the same anesthetic bath for the remaining experiments. The unpunctured and punctured suckers designated for amputated arm tests were randomized to control for the effect of time elapsed, postamputation. The suckers selected for the amputated arm with punctured sucker test were pierced using a 0.6 mm needle with a 0.3 mm tip diameter. Inserting the needle into the sucker orifice, four piercings were made along the acetabulum sidewalls, radially spaced.

Once all pull-off force tests were completed for the selected arm, the arm length and selected sucker rim diameters were measured using a metric ruler and digital caliper, respectively. The arm was then preserved in 10% neutral buffered formalin for future anatomical studies.

## 2.7. Data Analysis

After experimentation, data anomalies were discarded in the following manner. The coefficient of variation (i.e., ratio of standard deviation to mean) was calculated for each set of three independent sucker readings (per arm, per condition). A histogram of all coefficients of variation (CV) was then plotted, revealing a bimodal distribution with a global maximum at 1 and a secondary peak at 1.8, separated by a relative minimum at 1.5 (Figure S3, Supporting Information). As the higher mode may reflect anomalously deviant measures, all sets of three-sucker readings with CV above 1.5 were removed from the analysis. To test for factors affecting pull-off force, a linear mixed model was fit to the data, using IBM® SPSS® Statistics 25. The dependent variable was pull-off force, log-transformed to achieve

normally distributed residuals. The independent fixed variables were condition (intact arm with unpunctured, amputated arm with unpunctured, or amputated arm with punctured suckers), right/left arm, anterior/posterior arm, and sex. Octopus and arm (nested within octopus) were included as random variables, to account for repeated measurements on each arm and each animal. Sucker diameter and octopus body mass were included as covariates. Pairwise comparisons were performed for the different experimental conditions. To avoid alpha inflation in these comparisons, the sequential Bonferroni correction was used. Normality was tested by normal probability plots of residuals. Residual versus fitted values were plotted to confirm constant variance and linearity. The results are reported as log-transformed values. Estimated means are reported with their standard errors.

### 3. Results

Experimental manipulation had a significant effect on sucker pull-off forces (Figure 3). Specifically, log forces were lower for suckers on intact arms ( $0.492 \pm 0.172$  mN) than for unpunctured suckers of amputated arms ( $0.796 \pm 0.174$  mN;  $p = 0.003$ ). On amputated arms, punctured suckers had lower log pull-off forces ( $0.560 \pm 0.175$  mN) than unpunctured suckers ( $p = 0.014$ ). Intact arms did not differ significantly from punctured suckers on amputated arms ( $p = 0.723$ ). In short, amputation by itself led to higher pull-off forces, but puncturing the suckers of amputated arms reduced these forces.

The results did not support differences in pull-off forces based on arm location (Figure 4). Some studies have indicated that octopuses primarily use their anterior arms for exploring,<sup>[69,70]</sup> while posterior arms are used more frequently during walking and crawling.<sup>[71–73]</sup> However, no significant difference

was observed between the log pull-off force of anterior arm suckers ( $0.635 \pm 0.180$  mN) versus posterior arm suckers ( $0.597 \pm 0.182$  mN;  $p = 0.774$ ). Furthermore, while some octopuses demonstrate a lateral bias,<sup>[69,70]</sup> no significant difference was observed between the log pull-off force of right arm suckers ( $0.534 \pm 0.182$  mN) versus left arm suckers ( $0.698 \pm 0.187$  mN;  $p = 0.286$ ).

Potential effects of sucker size were minimized by testing proximal suckers in animals of similar size. The effects of sucker diameter, body mass, and sex on the pull-off force were found to be statistically insignificant, with  $p$ -values of 0.584, 0.801, and 0.088, respectively.

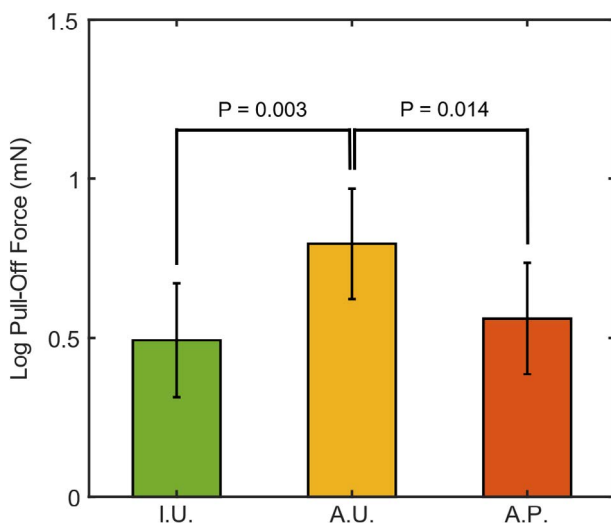
## 4. Discussion

### 4.1. Centralized versus Distributed Control

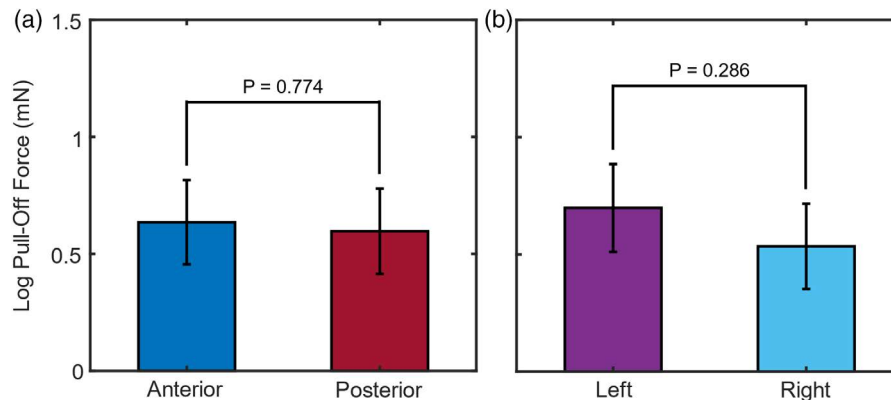
Perhaps the most notable observation from this study is the influence of centralized versus distributed control on sucker attachment and detachment. While sucker attachment is readily achieved in both intact and amputated arms, the mean pull-off force that is required to detach amputated arm suckers is significantly greater than that of intact arm suckers. This may suggest that the brain and/or interbrachial commissure trigger early sucker detachment in the intact animal, presumably to avoid sucker damage. Previous studies have alluded to this notion. After removal of the supraesophageal mass in the brain of *Octopus vulgaris*, Rowell observed: “under stress, e.g., when handled, it shows the phenomenon known as sticky suckers, in which the animal has difficulty in letting go of objects in contact with the suckers.”<sup>[44]</sup> More recently, Nesher et al.<sup>[59]</sup> observed that amputated arm suckers readily adhere to skinned arms, but never to arms with the skin intact, suggesting that sucker chemosensors are used to avoid arm interference and entanglement. In contrast, intact octopuses were observed to contact the skin of amputated arms, indicating that the brain or the interbrachial commissure is able to override reflexive arm responses. In the case of sucker detachment, it may be in the animal’s best interest to disengage from high pull-off forces to avoid sucker damage. Neural recordings of the sucker ganglia during sucker attachment and detachment for both intact and amputated arms may be a potential approach to confirm this hypothesis.

### 4.2. Suction versus Adhesion

Octopus suckers have been observed to adhere to both smooth and rough surfaces, as well as objects smaller and larger than the sucker diameter.<sup>[49,52]</sup> Based on the results of this study, sucker attachment is achieved by both adhesion and suction; however, suction plays the primary role. Suction is achieved when a pressure differential between the sucker (infundibulum and acetabulum) cavity and its surrounding environment is produced. By piercing the walls of the acetabulum, the sucker cavity, as defined by Tramacere et al.,<sup>[50,53,56]</sup> was compromised, and thus the pressure differential could not be generated. Minimal sucker pull-off force was subsequently detected, suggesting that suction plays a greater role in sucker attachment, although adhesion remains as a mechanism of attachment in a compromised sucker cavity.



**Figure 3.** Proximal sucker mean pull-off force of *O. bimaculoides* under different conditions. Intact arm with unpunctured sucker (I.U.;  $n = 90$ ), amputated arm with unpunctured sucker (A.U.;  $n = 91$ ), and amputated arm with punctured sucker (A.P.;  $n = 84$ ). Standard errors are provided for all mean values. Parameters: preload = 7 mN, contact time = 20 s, retract speed =  $0.4 \text{ mm s}^{-1}$ .



**Figure 4.** Proximal sucker mean pull-off force of *O. bimaculoides* with respect to arm grouping: a) anterior ( $n = 139$ ) versus posterior ( $n = 126$ ); b) right ( $n = 142$ ) versus left ( $n = 123$ ) arm suckers. Standard errors are provided for all mean values. Parameters: preload = 7 mN, contact time = 20 s, retract speed = 0.4 mm s<sup>-1</sup>.

Sucker adhesion may be achieved by the infundibulum's grooved and denticulated topography.<sup>[51–53]</sup> During our preliminary parameterization studies, the pull-off force of a sucker was observed to gradually decrease with each consecutive trial, dropping tenfold after the fourth trial (Figure S2a, Supporting Information). With each trial taking less than 2 min (on average) to complete and the preliminary parameterization studies showing sucker pull-off force on an amputated arm dramatically dropping only after a 46 min time-lapse (Figure S2b, Supporting Information), necrosis (i.e., death of tissue) could not be the main contributor to pull-off force reduction. Therefore, this may have been caused by damage to the sucker surface, hence the rationale for performing one trial per sucker in the reported pull-off force experiments. Kier and Smith<sup>[52]</sup> noted that a thin, single cuticle layer lines the infundibulum and acetabulum. Furthermore, Packard<sup>[74]</sup> stated that cuticle shedding occurs “to maintain the efficiency of the suckers as adhesive organs.” Therefore, it is quite possible that the cuticle layer contributes to the adhesion of the sucker. Furthermore, the mucus encompassing the sucker rim could also impact sucker adhesion.<sup>[52,75]</sup>

## 5. Conclusions

The observation of greater sucker pull-off forces in amputated versus intact arms may imply that the brain and/or interbrachial commissure play a critical role in sucker detachment. In addition, through piercing and compromising the sucker cavity, the pull-off force significantly decreased, suggesting that the primary mechanism for sucker attachment is suction, and is less dependent on adhesion. These insights into the control and function of octopus suckers can be integrated into the design and development of hierarchical control architectures and attachment mechanisms for soft robots performing manipulation and locomotion tasks in aquatic environments. However, before doing so, further studies are needed to investigate the degree of centralized versus distributed control mechanisms in octopuses and the degree to which their arms have evolved for specialized functions.

## Supporting Information

Supporting Information is available from the Wiley Online Library or from the author.

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## Conflict of Interest

The authors declare no conflict of interest.

## Keywords

adhesion, centralized control, distributed control, soft robotics, suction

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