RESEARCH ARTICLE

Octopus arm movements under constrained conditions: adaptation, modification and plasticity of motor primitives

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ABSTRACT

The motor control of the eight highly flexible arms of the common octopus (*Octopus vulgaris*) has been the focus of several recent studies. Our study is the first to manage to introduce a physical constraint to an octopus arm and investigate the adaptability of stereotypical bend propagation in reaching movements and the pseudo-limb articulation during fetching. Subjects (*N*=6) were placed inside a transparent Perspex box with a hole at the center that allowed the insertion of a single arm. Animals had to reach out through the hole toward a target, to retrieve a food reward and fetch it. All subjects successfully adjusted their movements to the constraint without an adaptation phase. During reaching tasks, the animals showed two movement strategies: stereotypical bend propagation reachings, which were established at the hole of the Perspex box and variant waving-like movements that showed no bend propagations. During fetching movements, no complete pseudo-joint fetching was observed outside the box and subjects pulled their arms through the hole in a pull-in like movement. Our findings show that there is some flexibility in the octopus motor system to adapt to a novel situation. However, at present, it seems that these changes are more an effect of random choices between different alternative motor programs, without showing clear learning effects in the choice between the alternatives. Interestingly, animals were able to adapt the fetching movements to the physical constraint, or as an alternative explanation, they could switch the motor primitive fetching to a different motor primitive 'arm pulling'.

KEY WORDS: Octopus, Reaching, Fetching, Motor control, Motor primitives

INTRODUCTION

Octopuses represent an interesting model for the research of motor control in a soft-bodied animal because they have eight highly flexible arms and a centralized nervous system. Recently, octopuses have been a model for developing bio-inspired robots with highly flexible continuum appendages (Zheng et al., 2013; Pfeifer et al., 2014).

The lack of any skeletal structure (Feinstein et al., 2011) enables the animals to move their arms in any direction, they can bend, twist, elongate and shorten and use virtually infinite degrees of freedom (DOF) (Kier and Smith, 1985). To reduce the complexity of arm control, the octopus uses motor primitives to perform stereotypical motor patterns. Motor primitives are loosely defined as the building blocks of a complex motion (Flash and Hochner, 2005), like an alphabet of elementary actions (Del Vecchio et al., 2003). Although the motor primitives themselves are considered invariant, they can be recombined dynamically to form complex movements (Moro et al., 2012).

Two discrete, stereotypical movements have been described in the octopus: 'bend propagation reaching' and 'pseudo-joint fetching'. While reaching toward a target, a bend propagates in a wave-like manner from the base of the arm toward the tip (Gutfreund et al., 1996). During these arm extension movements, motor neurons of the nerve cord activate the muscles in a wave-like manner and propagate the bend (Gutfreund et al., 1996, 1998). This stereotypical movement can also be elicited by stimulation of the nerve cord in an *in vitro* preparation, which demonstrates that the respective motor program is embedded in the arm of the octopus (Sumbre et al., 2001).

To fetch an object to their mouth, animals form quasi-articulated limbs based on three dynamic joints (Sumbre et al., 2005). Here, two waves of muscle activation travel toward each other and set a pseudo-joint location at their point of collision (Sumbre et al., 2006). This emulates the situation in vertebrate arms with stiffened joints and enables the octopus to use precise point-to-point movements. Both reaching and fetching, are highly stereotypical and greatly reduce the number of DOF and therefore the complexity of movement control.

One of the most important questions concerns the limitations of the octopus motor control system. To generate goal-directed movements, both robustness and adaptivity are equally important. Strict feed-forward motor programs are a trade-off between reduction of complexity and flexibility. This trade-off could be compensated by higher-order motor centers, but little is known about such adaptations in the control system of the octopus.

The basal lobes, which are the higher motor centers in the octopus (Young, 1971; Wells, 1978), consist of about 2.5 million cells, but seem to lack somatotopical organization at this level (Zullo et al., 2009), which suggests reduced interconnections of sensory and motor neurons. The large number of neurons in axial nerve cords of the arms, by contrast, may indicate an alternative control center for high-level information processing: The peripheral nervous system contains about 350 million cells, comprising about two-thirds of all neurons in the octopus. Most of the cells are located in axial nerve cords projecting from the brain to the arms (Budelmann, 1995). While a special division of labor between the central nervous system and the peripheral nervous system of the arms has been demonstrated before (Altman, 1971; Wells, 1978; Sumbre et al., 2001, 2005), lesion studies suggest that, at least in goal-directed movements, higher brain areas are necessary to control planning and execution of the motion, for example, during fetching motions (Sumbre et al., 2006).

It is unknown to what extent reaching and fetching movements can be controlled to overcome a physical constraint. To investigate the flexibility and adaptability of the motor control system, we

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introduced a physical constraint to the arm and studied how it affects the previously described behaviors bend propagation reaching and pseudo-joint fetching. The limitation to the onset of the motor primitives forced the animals to adapt to the new situation. Animals were able to adapt to the constraint by dynamically generating feed-forward bend propagation reaching movements and stereotypical pull-in fetching movements. These results show that octopuses have a flexible and dynamic motor control system, which adapts instantly to new situations.

RESULTS

Six octopuses were placed in a Perspex box and were required to reach toward a target and fetch the food reward by inserting their arm through a hole in the box. All animals were able to adapt to the physical constraint and used distinct strategies during the reaching (Fig. 1A) and fetching tasks (Fig. 1B). Overall, 286 successful reaching movements and 382 fetching movements were observed.

Reaching

During reaching tasks, octopuses used motions that were classified into two strategies: a straight point-to-point reaching (supplementary material Movie 1) and a seemingly undirected movement we termed waving-like (supplementary material Movie 2). Straight reaching movements (N=148) are linear point-to-point and goal-directed bend propagation reaching movements as first described by Gutfreund et al. (1996), complemented by elongation of the arm. The octopus positions the midsection of an arm over the hole of the Perspex wall and forms a loop outside of the box (Fig. 1A, seconds 0.3–1). This loop initiates the new bend, which will then travel toward the tip of

the arm (see Fig. 1A, seconds 1.4–2.4). Next to loop-induced bend propagation movements, bend propagations were set up freely outside the box in about 7% of all successful reaching movements. In these cases, the arm was put through the hole in a different manner (e.g. by stretching and pushing the tip of the arm through the hole) and a bend was established outside the box without the loop-building procedure at the hole.

In order to compare straight reaching motions in constrained situations with the unconstrained motions described by Gutfreund et al. (1996), the same analysis and normalization methods were used on ten random reaching movements, which successfully hit the target. The normalized tangential velocity profiles of constrained reaching movements showed typical invariant bell-shaped curves (Fig. 2B) with three corresponding phases, identical to reaching movements in an unconstrained situation (Fig. 2A). Phase I corresponds to the establishment of the bend and is the most variable part of the movement. Phase II, the propagation of the bend along the arm, corresponds to the steep velocity increase in the profile and is the most robust part of the movement. The maximum and subsequent decrease of velocity in phase III corresponds to a passive part of the movement in the vicinity of the object.

Waving-like movements (N=138) are seemingly undirected, explorative movements outside the box with no bend propagation and random kinematic profiles (Fig. 3). In most cases, the arm is put through the hole by using the loop-building procedure similar to movements in the straight category.

The reaching strategies differed significantly in the duration until the object was touched (Mann–Whitney U=312, N=272, P<0.001, Fig. 4), in which mean duration for straight bend
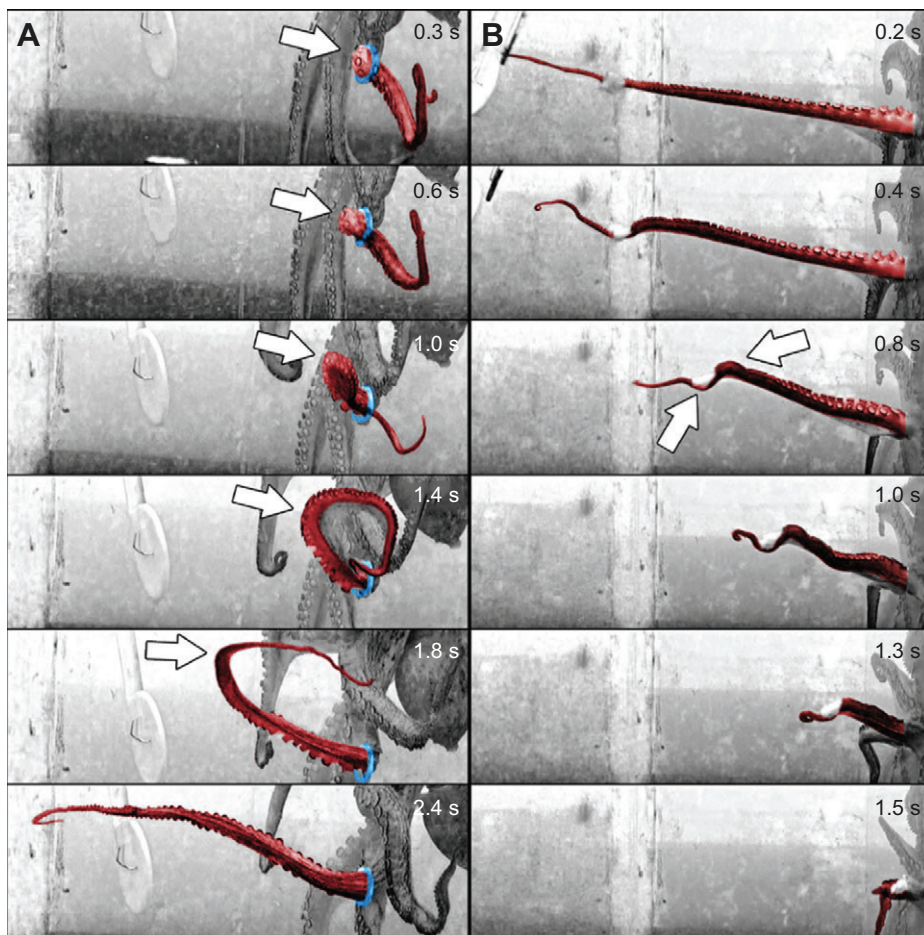

Fig. 1. Picture sequence of typical straight reaching and fetching movements of octopus arms in a constrained situation. Octopuses are behind a Perspex wall and reach or fetch through a hole with a single arm (indicated in red). (A) Straight reaching toward a target is done with a typical bend propagation, which is set up by building up an arm loop at the hole. White arrow indicates arm bend. Seconds 0.3–0.6 show building up of the arm loop; seconds 1.4–1.8 show bend propagation toward the target; 2.4 s frame shows arm hitting the target. Blue ring highlights the hole. (B) Straight fetching of a food item (white object). Frame at 0.2 s shows the arm attached to target; seconds 0.4–1.5 show linear point-to-point pull-in movement. Arrows at 0.8 s mark two bends of the S-shaped grip of the food item (white). Colors, brightness and contrast were altered to highlight arm movements.
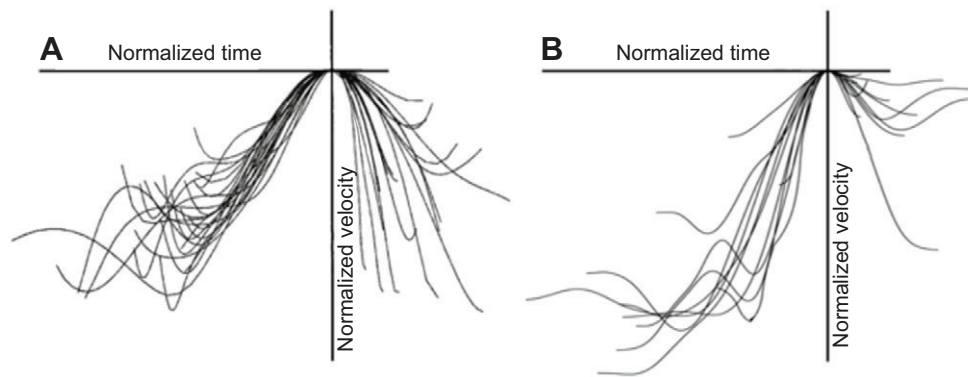
Fig. 2. Comparison of normalized tangential velocity profiles during reaching tasks. (A) Unconstrained animals (taken from Gutfreund et al., 1996) and (B) constrained animals. Both graphs show bell-shaped curves, aligned at peak velocity and with axes normalized for time and velocity.

propagation reachings was short (2.4±1.3 s) and longer for waving-like motions (12.4±7.1 s). While waving-like behavior was observed more often than straight bend propagation reaching on average (N=130±109 and 29±19, respectively), the success rate was higher for straight reachings (87±11.4%) than for waving-like motions (27.7±29.8%).

Since straight reachings were more successful, learning in the octopuses might mean a transfer of their strategy from a more undirected and waving-like movement to an efficient point-to-point reaching. To test whether a shift in reaching strategies happened over time, strategy choices were compared between the beginning and the end of the experiments. Successful reaching motions were split into three trial bins for each animal and then compared between first and last bins (Fig. 5). Two of six animals significantly changed the strategy in the last third of the experiment compared with the first; in the last third of the experiment, animal 5 increased the amount of waving-like motions (χ_1^2=6.65, N=30, P=0.01) and animal 3 increased the amount of straight reachings (χ_1^2=7.84, N=74, P=0.005). The relative number of fails did not change over the course of the experiment (χ_1^2=3.043, N=634, P=0.081).

Fetching

All animals were able to pull the food reward through the hole in the Perspex wall and only a few trials were marked as fails (food dropped, N=24; general execution error, N=5). To test for differences in movement patterns, all movements were subjectively categorized into two categories, straight (supplementary material Movie 3) or deflected (supplementary material Movie 4) movements. Movements that showed a general immediacy and an overall straight and point-to-point shape were classified as straight movements and movements that could not clearly be classified as straight movements formed the deflected group. To differentiate the two categories in order to

test whether these movements are discrete, a sample of 60 successful fetching trials (ten per animal) were tested for general reliability of the classification into categories. First, the movements were reevaluated by subjective categorization of a second observer and then by a categorization based on 3D reconstruction of the movements' trajectories and their tangential velocity profiles.

To test for inter-rater reliability of the subjective categorization, Krippendorff's α (Hayes and Krippendorff, 2007) was calculated for two observers. The classification was accepted with an agreement of α=0.67 (95% CI, 0.443 to 0.851). The relatively vague criteria for classification justified the use of the minimum recommended α-values (Hayes and Krippendorff, 2007).

Movements with generally straight trajectories were categorized as straight (Fig. 6A), as well as normalized tangential velocity profiles that showed stereotypic bell-shaped curves (Fig. 6B). Trajectories and tangential velocity profiles that were random and not stereotypical were categorized as deflected (Fig. 6C,D). The three ratings per movement, based on subjective categorization, tangential velocity profiles and trajectories were tested for compliance and showed a general consent on their respective categorization (Krippendorff α=0.71). Overall 281 trials were categorized as straight and 100 as deflected.

Mean fetching times also differed significantly between categories (Mann–Whitney U=21.5, N=381, P<0.001), with a mean duration of 2.7±1.66 s for the straight category and 5.81±4.82 s for the deflected category.

The distribution of the strategies during the first ten trials was not homogenous among the animals (Table 1). Four of the six animals showed straight fetching in the first trial and the general distribution of strategies was found to be random (One-sample runs test, not significant; see Table 1).
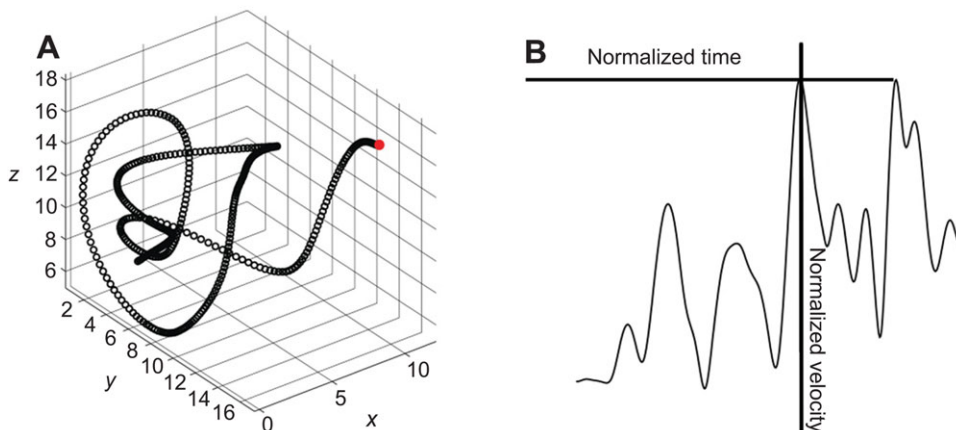

Fig. 3. Kinematic profiles of typical waving-like motions. (A) 3D reconstruction of the trajectory of an arm. One circle represents the site of the attached food item on the arm in a single frame of a picture sequence with 25 f.p.s. Red circle indicates the site of the target. The axes show distances in cm. (B) Normalized tangential velocity profile.
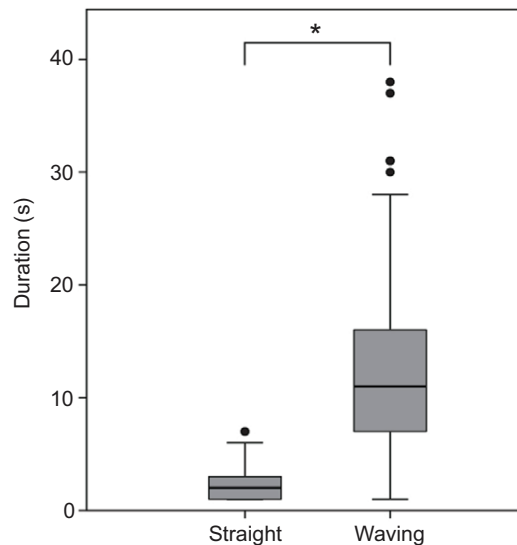
Fig. 4. Comparison of reaching durations. Duration of reaching in the straight and waving-like categories. *$P<0.05$.

To test if the animals changed their fetching strategies during the course of the entire experiment because of an adaptation to the constraint, all trials were divided into three trial bins for each animal and the respective movement categories were analyzed (Fig. 7). The relative number of straight and deflected fetches did not change significantly from the first to the last third of the experiment ($\chi^2_1=1.748$, $N=254$, $P=0.1869$). Also, the combined fetching time of all animals showed no significant improvement ($U=8752$, $N=253$, $P=0.191$); however, two individual animals significantly changed their mean fetching time during the experiment: animal 2 lowered the mean fetching time from 7.24 ± 5.5 s in the first third to 3.85 ± 3.5 s in the last third of the experiment ($U=69.5$, $N=34$, $P=0.009$) but animal 5 raised it from 1.71 ± 0.75 s to 2.45 ± 1.1 s ($U=1015$, $N=75$, $P=0.001$). These two opposed changes in reaching time point toward individual, rather than general effects.

DISCUSSION

A very promising perspective to explain movement generation and to overcome the motor equivalence problem of increasing complexity with increasing DOF (Bernstein, 1967) is the modular approach. Movements result from the combination of a finite set of stable motor primitives (Bizzi et al., 2008) or a stereotypical co-activation of several muscles, called muscle synergies (d'Avella et al., 2003). Several studies showed the use of robust motor primitives during reaching (Gutfreund et al., 1996) and fetching movements (Sumbre et al., 2005) of unrestrained octopuses. However, there are no studies on the plasticity of movements and adaptivity of movement control. Our study is the first to manage to introduce a physical constraint to the octopus arm. This enabled us to gain new insights into the ability of the motor system to adapt and modify the motor primitives bend-propagation reaching and pseudo-joint fetching.

Adaptation to constraints

All animals adapted to the physical constraint and were able to reach and fetch through the hole in the Perspex wall. The animals showed flexibility in movement control by adapting to the constraint and using an appropriate movement to get to the food reward. In order to elucidate learning effects, movements of the reaching and fetching tasks were categorized into variant and invariant movements. Invariant movements had stereotypical kinematic profiles with straight trajectories and bell-shaped tangential velocity profiles. Variant movements were described as 'waving-like reaching' and 'deflected fetching' and had no stereotypical trajectories, variable tangential velocity profiles and were longer in duration.

As there is no significant change in the number of these movements over the course of the experiments, we assume that these movements are not transitional states during an adaptation period (Arce et al., 2009). Only one animal changed its behavior toward the more efficient straight reaching strategy, despite the higher success probability. Likewise, during fetching tasks, animals did not entirely change to the faster 'pull-in' movements. Interestingly, the relative number of fails, which presumably represented explorative movements without coincidental target hits, also did not change over the course of the experiment per animal, which suggests an absence of learning effects (Sosnik et al., 2004) or an insufficient motivational state of the animal to trigger learning effects. The general absence of any clear learning effect in terms of improvement in performance or in terms of time taken to complete a task suggests an absence of the ability of *Octopus vulgaris* to shape motor programs due to learning. Since these behaviors must then be innate, the variance in the strategies suggests
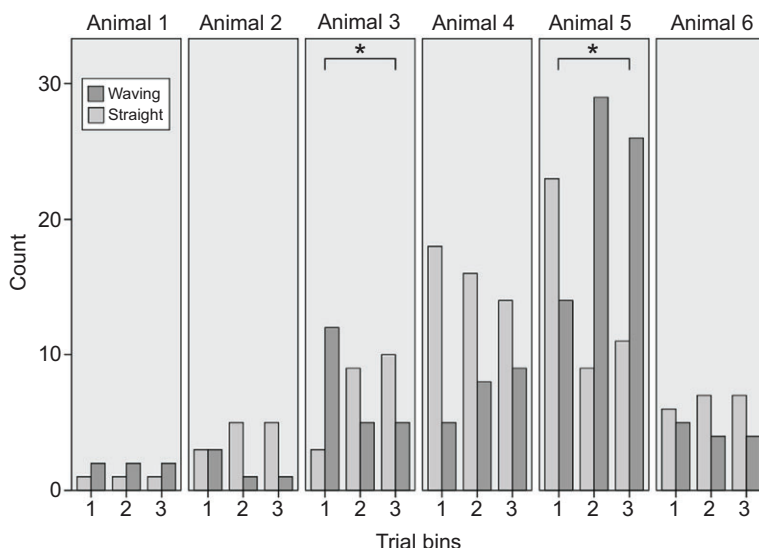

Fig. 5. Number of choices in waving and straight reaching categories, split into three trial bins for each animal. Significant differences between the first and third trial bin were recorded in animal 3 and animal 5. *$P<0.05$.
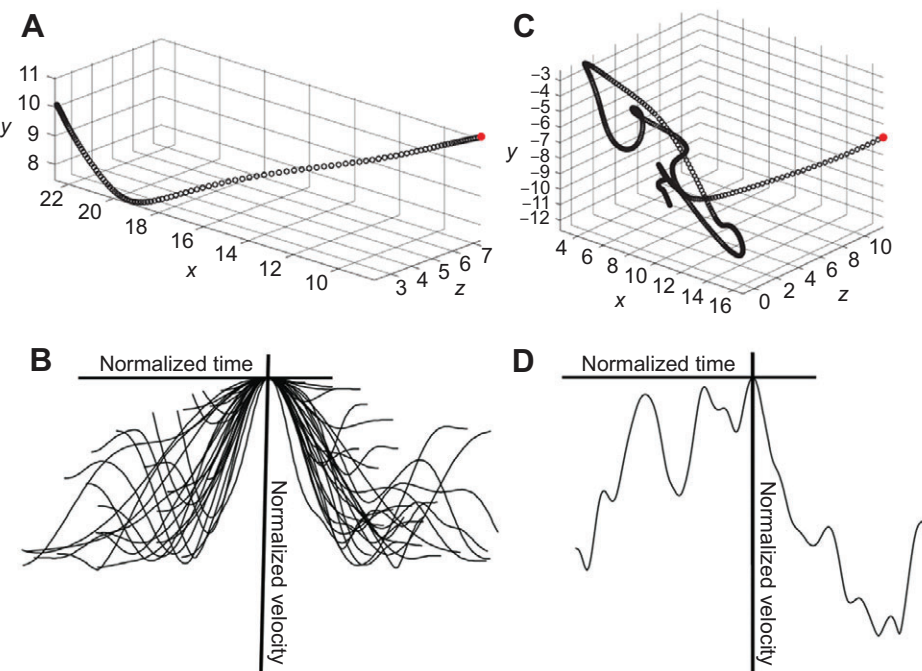
Fig. 6. Kinematic profiles of straight and deflected fetching categories. 3D reconstruction of typical arm trajectories for (A) straight fetching and (C) deflective fetching categories. One circle represents the site of the attached food on the arm in a single frame of a picture sequence with 25 f.p.s. Red circles indicate the site of the hole. Axes show distances in cm. (B) Normalized tangential velocity profiles for straight fetching movements. (D) One trial is shown for clarity in the deflected category.

that the animals switch between different movement strategies during the same condition. In general, the waving-like reaching and the variances in the fetching patterns showed that the octopus' movement repertoire is probably not limited to a fixed set of movements. At least in the waving-like movements, the high number of observations (N=130±109) and low success rate (about 25%) compared with straight reachings (N=29±19; about 85% success rate) might explain the movement as an explorative movement, in which the animal touched the target by accident.

Stereotypical movements

Movements of the reaching and fetching tasks were categorized according to their kinematic profiles or movement patterns. Stereotypical movements were generally immediate and goal-directed movements with straight trajectories.

During reaching tasks, the animals used propagating bends that were either initiated by building up loops through the hole of the wall using the approximate midsection of the arm, or were freely initiated outside the box. These bend propagation movements showed linear trajectories and stereotypical invariant normalized tangential velocity profiles and were identical to movements in

freely behaving animals (Gutfreund et al., 1996). The dynamic range of control over this robust feed-forward motor program has not been shown before in the octopus: the animals were able to sequentially connect the motor primitive bend propagation reaching and the loop building at the hole of the wall, which could even be initiated outside the box. Since loop building at the hole was also observed in most movements of the waving category, it should be seen as an independent movement from the bend propagation initiation. Our findings suggest that the octopus can start the motor primitive at any point along the arm and subsequently hit the target. This is an important finding because it stands in contrast to a previous hypothesis which proposed that the directional control of the reaching movement is determined by adjusting two DOF (yaw and pitch) at the base of the arm (Gutfreund et al., 1996).

Fetching movements categorized as straight consisted of a single linear motion. They were done with straight point-to-point pull-ins of the arms, with straight trajectories and bell-shaped normalized tangential velocity profiles. These movements differ from fetching movements in freely behaving animals, because in our experiments no formation of stereotypical pseudo joints and quasi-articulated limbs could be observed. Interestingly, the kinematic profiles of

Table 1. Distribution of categories among the first ten trials

|	Animal 1	Animal 2	Animal 3	Animal 4	Animal 5	Animal 6
Trial						
1	Deflected	Deflected	Straight	Straight	Straight	Straight
2	Deflected	Deflected	Deflected	Deflected	Straight	Straight
3	Deflected	Straight	Straight	Straight	Straight	Straight
4	Deflected	Deflected	Deflected	Straight	Straight	Straight
5	Deflected	Deflected	Straight	Straight	Straight	Straight
6	Deflected	Straight	Straight	Straight	Straight	Straight
7	Deflected	Straight	Straight	Straight	Straight	Deflected
8	Straight	Deflected	Straight	Straight	Deflected	Straight
9	Deflected	Straight	Deflected	Straight	Straight	Straight
10	Straight	Straight	Straight	Deflected	Deflected	Deflected
One-sample runs test						
r	4	6	7	4	4	4
P	1	1	0.287	1	1	1
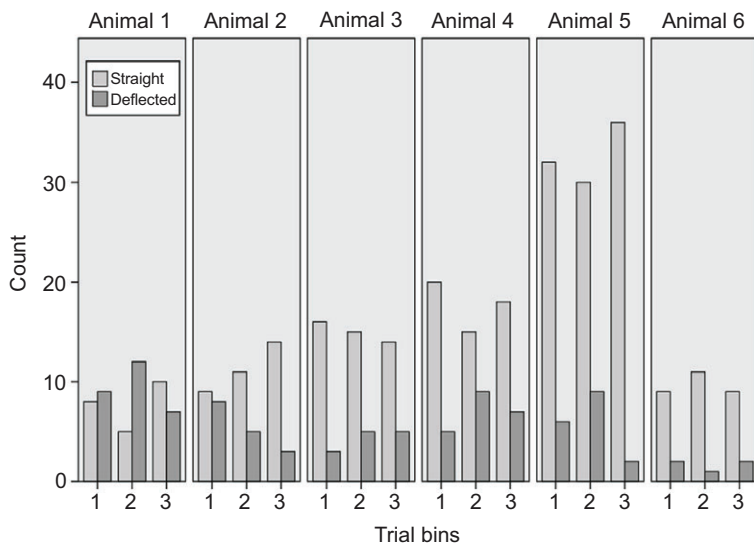
Fig. 7. Number of choices in straight and deflected fetching categories, split into three trial bins for each animal. No significant differences were recorded between the first and third trial bin in each category per animal.

straight fetching movements were very similar to the stereotypical bend propagation reaching movements in freely behaving animals, suggesting that these fetching movements are complete and uninterrupted movements. This suggests that this is either a modification of the existing motor primitive or an as yet unknown new motor primitive – arm pulling.

Visual examination of all fetching movements showed a commonality between the two categories during fetching: in all trials the gripping shape of the arms seemed to be preserved and showed an S-shape, formed by the attachment of the food and an immediate second bend (see arrows in Fig. 1B, 0.8 s). This has been described before (Sumbre et al., 2005, 2006) as 'grasp of food item' and 'distal joint'. It is unclear, however, whether the grasping of the food item triggered pseudo-joint fetching, initiating, for example, the onset of medial and proximal joints, which might then have been masked or canceled by a conflicting feedback signal triggered by the constraint on the arm. To clarify this possibility, a further kinematic analysis would be required.

The neuromuscular control of the movement generation is unclear. It was hypothesized before, that the grip of the food item triggers two waves, which form pseudo-joints at the point of collision, creating dynamic joints along the arm with fixed ratios of inter-segment lengths (Sumbre et al., 2006). Although it is unclear if these joints were masked or canceled by higher-order control mechanisms in the constraint situation, they did not interfere with the immediate switch to a straight pull-in movement in some animals (see Table 1). Unfortunately, the proximal part and the base of the arm inside the box were not visible enough for a meaningful analysis of the pull-in mechanism. The food items might have triggered the onset of a medial and proximal bend at the very proximal part of the arm inside the box, which were then dynamically altered by sensory information in terms of the length and stiffness of the quasi-articulated structures.

Variant movements

Movements of each of the two stereotypical categories share similar motion patterns and seem goal directed because of the stereotypical kinematic profiles. However, the mechanisms underlying the movements in the variant category are unclear. The variant movements of the reaching tasks, categorized as waving-like movements, seemed to be fundamentally different from stereotypical bend propagation movements. Waving-like movements had random

kinematic profiles and were seemingly undirected and the successful reaching movements to the target were lower than the direct reaching movements, thus less rewarding. However, the movement patterns of variant fetching movements differed only marginally from stereotypic point-to-point fetching movements, although differences in the kinematic profiles and duration were observed. The trajectories seemed to be random deviations from linear trajectories and were thus labeled as deflected categories. A commonality of all fetching movements seemed to be a pull-in motion pattern, controlled by the proximal segment of the arm and by shortening the arm. In contrast to reaching movements, the reward gained by the two types of pulling were similar.

Point-to-point pull-in fetching movements with their stereotypical kinematic profiles, that is, linear trajectories and the bell-shaped normalized tangential velocity profiles, could present another motor primitive for situations where an arm is pulled through a tight opening. It is reasonable to assume that the pull-in movement itself was controlled by more-proximal parts of the arm, which were inside the box and, unfortunately, not visible enough for a meaningful analysis. A common mechanism for pull-in fetching movements could explain why the movement showed both, robust and variant forms and still seemed to have the same motion mechanics: while the proximal part of the arm controls the pull-in, the distal part is passive. Movement speed or immediacy of the pull-in movement changes the kinematic profile of the tip of the arm, which was the reference point during the kinematic analysis (see Materials and methods). The animal would then be able to switch between activating a pull-in motor primitive and active control of the distal part of the arm. This switch between robust motor primitives and flexible movements would be similar in principle to the dynamic linking of movement patterns during reaching movements in the constrained situation.

Sensory feedback

Whether octopuses are able to use sensory feedback to control their movements has been discussed previously (Wells, 1978; Gutfreund et al., 2006) and Gutnick et al. (2011) presented evidence that animals use visual feedback from their arms during three-choice-maze experiments. In our findings, tactile sensors might collect additional information on the arm. The restriction due to the hole should provide sensory information to recognize the restricted mobility of the arm and thus this information is used to generate appropriate movements to overcome the constraint. The lack of a systematic change in strategy

choices between the variant and stereotypical form of the respective movement implies that no trial-and-error learning phase occurred during the course of the experiment. In the fetching task, most animals used point-to-point pull-in motions without an adaptation phase. In the reaching task, the animals initiated the loop of the bend propagation at the hole, which suggests that they used sensory feedback to identify the dimensions of the obstacle and the point at which the initiation of the feed-forward motor program 'bend propagation reaching' was possible.

Since feedback-controlled movements are generally considered to be too slow for fast online correction (Kawato, 1999), we propose that the octopus uses sensory feedback to gather information about its environment and incorporate them in its feed-forward inverse model to compute adequate actions and trajectories. While no change in categories over the course of the experiment was recorded, which could have been an indication for trial-and-error learning, all animals explored the box and its opening extensively during the experiments.

Conclusions

The results of this study suggest that the octopus higher motor control system is flexible and adapts to novel situations mainly by choosing between two different movements that solve the task, albeit with different reward rates. Interestingly, despite the difference in reward rate in the reaching movement, no learning was demonstrated. This suggests that the reward does not affect the decision between the two types of reaching (waving and direct). An intriguing finding that requires further investigation is the demonstrated ability of the octopus to direct its arm to the target even though the movement starts from the hole rather than from the base of the arm. This proposes that the octopus uses sensory feedback to gather information about its environment and incorporates this in its feed-forward inverse model to compute adequate actions and trajectories. With respect to fetching, it seems that the octopus has two alternative behaviors to solve the task (direct and indirect pulling). In this task, there also seems to be a fixed decision ratio that also does not change over time (but here the reward is equal for the two movements).

MATERIALS AND METHODS
Subjects and holding experiments
Subjects were six wild-caught *Octopus vulgaris* (Lamarck 1798) (2 females, 4 males; 250–450 g bodyweight) collected by fishermen from the Israeli coast of the Mediterranean Sea. The animals were housed individually in 100 l artificial sea water tanks within a closed circulation system and held according to the guidelines for the EU Directive 2010/63/EU for cephalopod welfare (Fiorito et al., 2014). Tanks were enriched with clay-pot dens, gravel, rocks and green algae (*Caulerpa prolifera*); the temperature of the holding rooms was held constant at about 19°C. Day and night cycles were simulated by artificial illumination for 12 h:12 h, light:dark. Animals were fed every other day with either dead shrimps or pieces of fish.

All animals were acclimatized for at least 14 days in the holding tanks before they were transferred to an experiment tank (400 l), where they were acclimatized for another day before experiments started. Animals were preselected for motivation and general health.

Each animal was placed separately inside a custom-made transparent Perspex box (40×40×40 cm) with a hole (1.5 cm in diameter) at the center of one side that allowed the insertion of only a single arm. The animal had to reach out through the hole to retrieve a food reward and pull it back in. Success criterion for the reaching task was the touching of a target (white Perspex disc on a transparent Perspex stick). A piece of shrimp was placed on the tip of the arm, which had to be completely pulled through the hole for a successful fetching task. The reaching task onset was marked by the insertion of the target into the water. Fetching tasks followed successful

reaching tasks or were initiated by letting the animal grip the target and then being pulled to stretch the arm to average fetching distance. The target was presented approximately at the level of the hole and the distance varied between 2 and 40 cm to motivate the animals to reach for it.

Kinematic analysis
The experiment was constructed according to the publication by Gutfreund et al. (1996). The sessions were recorded with two digital video cameras (Sony Handycam HDR-XR550; Tokyo, Japan) in an angle of about 90 deg and later formatted, cut and transformed into picture sequences (25 frames per second) with video editing software (Adobe Premiere CS5; San Jose, California, USA).

For the 3D reconstruction of trajectories and tangential velocity profiles, the visual information of the two cameras was transformed to 3D coordinates, applying the direct linear transformation (DLT) method (Wood and Marshall, 1986; Woltring and Huiskes, 1990). A calibration body was used to obtain 11 parameters that were used to define the image coordinates of the two cameras in the following DLT equations:

$$x_1 = \frac{P_1 X + P_2 Y + P_3 Z + P_4}{P_9 X + P_{10} Y + P_{11} Z + 1}, \quad (1)$$

$$y_1 = \frac{P_5 X + P_6 Y + P_7 Z + P_8}{P_9 X + P_{10} Y + P_{11} Z + 1}, \quad (2)$$

with x_1 and y_1 as image coordinates of a designated point of camera 1 and the unknown 3D coordinates X, Y and Z. The variables P_1–P_{11} represent the 11 parameters obtained from defined points of the calibration body.

Three points of interest were then marked in the image sequences using MATLAB (MathWorks; Natick, MA, USA) to reconstruct arm movement: two reference points and either the bend or tip of the arm during reaching tasks, or the food item, which was typically put on the distal quartile of the arm during fetching tasks. This positional data was then used to calculate the tangential velocity profile. The data was smoothed by fitting a fifth-order polynomial to the projections of the points on the three axes as a function of time. The coefficients were obtained by calculating the least-square equation, using the singular value decomposition algorithm. Then V_{tan} was calculated from the derivatives of the smoothed coordinates $X(t)$, $Y(t)$ and $Z(t)$ with:

$$V_{\text{tan}} = \sqrt{\left(\frac{dX}{dt}\right)^2 + \left(\frac{dY}{dt}\right)^2 + \left(\frac{dZ}{dt}\right)^2}. \quad (3)$$

To account for invariances, the tangential velocity [$V(t)$] and time (t) were normalized according to the maximum velocity (V_{max}) and travel distance (D), following procedure after Atkeson and Hollerbach (1985) and Gutfreund et al. (1996):

$$V_{\text{normalized}} = \frac{V(t)}{V_{\text{max}}}, \quad (4)$$

$$T_{\text{normalized}} = \frac{V_{\text{max}} \times t}{D}, \quad (5)$$

$$D = \sum_t \sqrt{(X_t - X_{t-1})^2 + (Z_t - Z_{t-1})^2}, \quad (6)$$

with the smoothed coordinates X and Z and the index t as image number or time.

Further data analysis was done with SPSS 19 (IBM Software; Armonk, NY, USA) and Microsoft Excel 2011 for Mac OS (Redmond, Washington, USA). An inter-rater reliability test was done in order to calculate rating similarities between two independent observers. For this purpose, two observers categorized the same trials according to the categorization rules and differences were calculated according to Hayes and Krippendorff (2007).

Supplementary material
Supplementary material available online at
http://jeb.biologists.org/lookup/suppl/doi:10.1242/jeb.115915/-/DC1
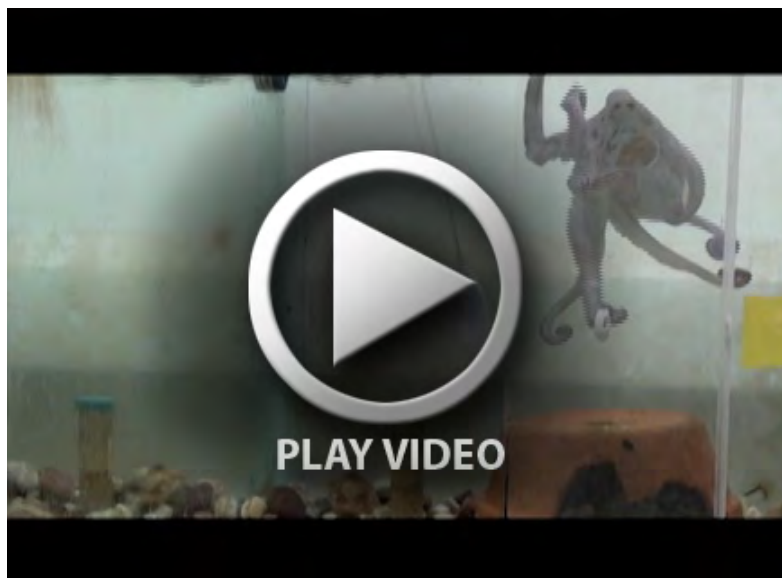
References

Altman, J. S. (1971). Control of accept and reject reflexes in the octopus. *Nature* **229**, 204-206.

Arce, F., Novick, I., Shahar, M., Link, Y., Ghez, C. and Vaadia, E. (2009). Differences in context and feedback result in different trajectories and adaptation strategies in reaching. *PLoS ONE* **4**, e4214.

Atkeson, C. G. and Hollerbach, J. M. (1985). Kinematic features of unrestrained vertical arm movements. *J. Neurosci.* **5**, 2318-2330.

Bernstein, N. A. (1967). *The Co-ordination and Regulation of Movements*. Oxford: Pergamon Press.

Bizzi, E., Cheung, V. C. K., d'Avella, A., Saltiel, P. and Tresch, M. (2008). Combining modules for movement. *Brain Res. Rev.* **57**, 125-133.

Budelmann, B. U. (1995). The cephalopod nervous system: what evolution has made of the molluscan design. In *The Nervous Systems of Invertebrates: An Evolutionary and Comparative Approach*, vol. 72 (ed. O. Breidbach and W. Kutsch), pp. 115-138. Basel: Birkhäuser.

d'Avella, A., Saltiel, P. and Bizzi, E. (2003). Combinations of muscle synergies in the construction of a natural motor behavior. *Nat. Neurosci.* **6**, 300-308.

Del Vecchio, D., Murray, R. M. and Perona, P. (2003). Decomposition of human motion into dynamics-based primitives with application to drawing tasks. *Automatica* **39**, 2085-2098.

Feinstein, N., Nesher, N. and Hochner, B. (2011). Functional morphology of the neuromuscular system of the octopus vulgaris arm. *Vie Milieu* **61**, 219-229.

Fiorito, G., Affuso, A., Anderson, D. B., Basil, J., Bonnaud, L., Botta, G., Cole, A., D'Angelo, L., De Girolamo, P., Dennison, N. et al. (2014). Cephalopods in neuroscience: regulations, research and the 3Rs. *Invert. Neurosci.* **14**, 13-36.

Flash, T. and Hochner, B. (2005). Motor primitives in vertebrates and invertebrates. *Curr. Opin. Neurobiol.* **15**, 660-666.

Gutfreund, Y., Flash, T., Yarom, Y., Fiorito, G., Segev, I. and Hochner, B. (1996). Organization of octopus arm movements: a model system for studying the control of flexible arms. *J. Neurosci.* **16**, 7297-7307.

Gutfreund, Y., Flash, T., Fiorito, G. and Hochner, B. (1998). Patterns of arm muscle activation involved in octopus reaching movements. *J. Neurosci.* **18**, 5976-5987.

Gutfreund, Y., Matzner, H., Flash, T. and Hochner, B. (2006). Patterns of motor activity in the isolated nerve cord of the octopus arm. *Biol. Bull.* **211**, 212-222.

Gutnick, T., Byrne, R. A., Hochner, B. and Kuba, M. (2011). Octopus vulgaris uses visual information to determine the location of its arm. *Curr. Biol.* **21**, 460-462.

Hayes, A. F. and Krippendorff, K. (2007). Answering the call for a standard reliability measure for coding data. *Commun. Methods Measures* **1**, 77-89.

Kawato, M. (1999). Internal models for motor control and trajectory planning. *Curr. Opin. Neurobiol.* **9**, 718-727.

Kier, W. M. and Smith, K. K. (1985). Tongues, tentacles and trunks: the biomechanics of movement in muscular-hydrostats. *Zool. J. Linn. Soc.* **83**, 307-324.

Moro, F. L., Tsagarakis, N. G. and Caldwell, D. G. (2012). On the kinematic Motion Primitives (kMPs) - theory and application. *Front. Neurorobot.* **6**, 10.

Pfeifer, R., Iida, F. and Lungarella, M. (2014). Cognition from the bottom up: on biological inspiration, body morphology, and soft materials. *Trends Cogn. Sci.* **18**, 404-413.

Sosnik, R., Hauptmann, B., Karni, A. and Flash, T. (2004). When practice leads to co-articulation: the evolution of geometrically defined movement primitives. *Exp. Brain Res.* **156**, 422-438.

Sumbre, G., Gutfreund, Y., Fiorito, G., Flash, T. and Hochner, B. (2001). Control of octopus arm extension by a peripheral motor program. *Science* **293**, 1845-1848.

Sumbre, G., Fiorito, G., Flash, T. and Hochner, B. (2005). Neurobiology: motor control of flexible octopus arms. *Nature* **433**, 595-596.

Sumbre, G., Fiorito, G., Flash, T. and Hochner, B. (2006). Octopuses use a human-like strategy to control precise point-to-point arm movements. *Curr. Biol.* **16**, 767-772.

Wells, M. J. (1978). *Octopus. Physiology and Behaviour of an Advanced Invertebrate*. London: Chapman and Hall.

Woltring, H. J. and Huiskes, R. (1990). Stereophotogrammetry. In *Biomechanics of Human Movement: Applications in Rehabilitation, Sports and Ergonomics* (ed. N. Berme and A. Cappozzo), pp. 108-127. Worthington, OH: Bertec.

Wood, G. A. and Marshall, R. N. (1986). The accuracy of DLT extrapolation in three-dimensional film analysis. *J. Biomech.* **19**, 781-785.

Young, J. Z. (1971). *The Anatomy of the Nervous System of Octopus vulgaris*. Oxford: Clarendon Press.

Zheng, T., Branson, D. T., Guglielmino, E., Kang, R., Cerda, G. A. M., Cianchetti, M., Follador, M., Godage, I. S. and Caldwell, D. G. (2013). Model validation of an octopus inspired continuum robotic arm for use in underwater environments. *J. Mech. Robot.* **5**, 021004.

Zullo, L., Sumbre, G., Agnisola, C., Flash, T. and Hochner, B. (2009). Nonsomatotopic organization of the higher motor centers in octopus. *Curr. Biol.* **19**, 1632-1636.

Movie 1. Reach. This movie clip shows a typical straight and stereotypical reaching movement with a bend propagation. A loop forms at the site of the hole, which then is the basis for the following bend propagation toward the target.

Movie 2. Waving. This movie clip shows a variant and non-stereotypical reaching movement termed 'waving', which is not directly aimed at the target.

Movie 3. Fetch. This movie clip shows a typical straight and stereotypical fetching movement, a direct pulling-in of the arm.
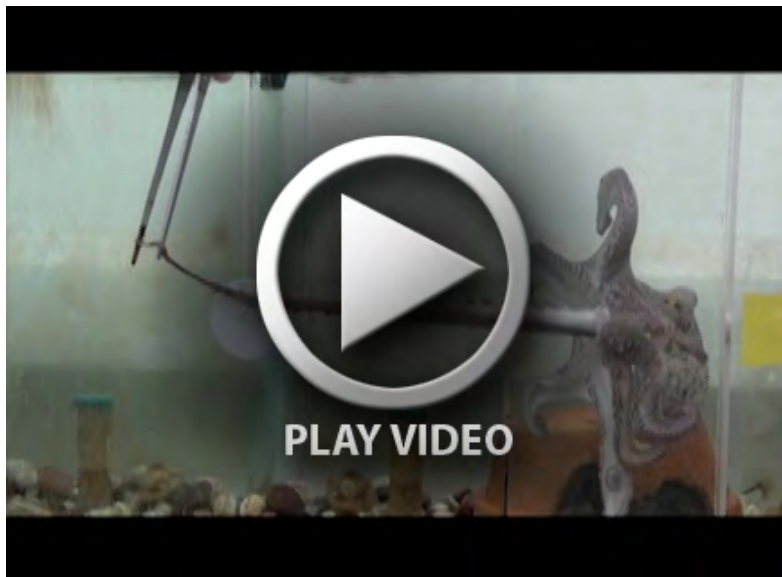
Movie 4. Deflected. This movie clip shows a variant form of the fetching movement, termed 'deflected'. The subject is not fetching in a single movement.
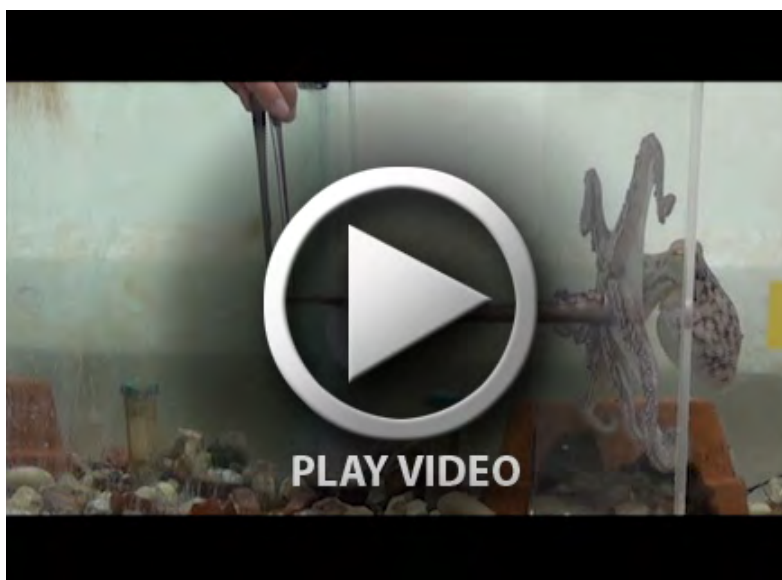

Movie 1.

Movie 2.

Movie 3.

Movie 4.