How to move with no rigid skeleton?

The octopus has the answers?

Yoram Yekutieli, German Sumbre, Tamar Flash and Binyamin Hochner
Hebrew University, Jerusalem and Weizmann Institute of Science, Rehovot, Israel.

The octopus is amazingly flexible and shows exceptional control and coordination in all its movements. It seems remarkable to us skeletal creatures that the octopus achieves all this without a single bone.

Imagine yourself swimming freely near the seabed, exploring the coral reef with your excellent sense of vision and your eight flexible, boneless arms – touching and tasting the environment, squeezing into narrow passages while hunting for crabs and fish and other small creatures. In order to avoid being seen by either prey or predators, you change your skin colour and texture to blend with your surrounding. Suddenly, you spot a big shark heading directly towards you. You quickly release a dose of black ink to cover your escape and use your highly effective jet propulsion to accelerate and reach the nearest shelter. You are safe for now.

This is the world of the octopus. Almost every aspect of an octopus's life is different from ours, but we are curious enough to try to understand it. In this review, we focus on octopus arm movements, taking one stereotypical pattern of motion – the reaching movement – as an example of a recently studied movement in this remarkable creature.

Flexible arms

Octopuses and their relatives, squids and cuttlefish, belong to the group *Cephalopoda* (from Greek, kefalos = head and podos = foot), which are unique among molluscs. They have a sac-like mantle and a siphon used for breathing and jet propulsion, eight or ten appendages growing out of the head and reduced internal shells, which the octopus has completely lost. The octopus is a solitary predator that usually dwells near the seabed in rocky terrains. Octopus arms are extraordinary organs; they are able to exert great force and grip, move with a wide range of velocities and can delicately manipulate objects, all without any rigid skeletal element inside them.

Octopus arms, as well as elephant trunks, squid tentacles and vertebrate tongues are termed **muscular hydrostats** (Kier and Smith, 1985). In such structures, the volume of the organ remains constant during all movements (muscle fibres, as other biological cells, are incompressible), enabling the muscles themselves to perform all the functions usually performed by the skeleton. Such flexible structures show major advantages over articulated arms that have a rigid skeleton and joints, like our own. Muscular hydrostat arms can operate in highly constrained and complex environments by drastically changing their shape, bypassing obstacles and squeezing into narrow holes. Articulated arms would need a much wider clear space in order to operate successfully because their shape is limited by their skeletal elements.

Researchers in the field of robotics try to mimic the flexible and highly effective muscular hydrostat structures found in nature by building robotic manipulators with a large number of joints (Chirikjian and Burdick, 1994). These are termed **hyper redundant** manipulators because they have a large number of **degrees of freedom.** (If the relative motion between two parts can be described by one parameter then it has one degree of freedom: for

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Title image: An octopus reaching towards a target.

example, the state of a door rotating on its hinges. The human arm – not including the fingers – has seven degrees of freedom, while only six are needed to fully describe the position and orientation of the hand or an object it grasps in 3D space.) Hyper redundant manipulators have many more degrees of freedom than the minimal theoretical number needed for a given task. The problem, of course, is how to control this abundance of degrees of freedom. An appealing approach, generally known as biomimetics, is to look and learn from nature and try to use the new knowledge in novel engineering designs.

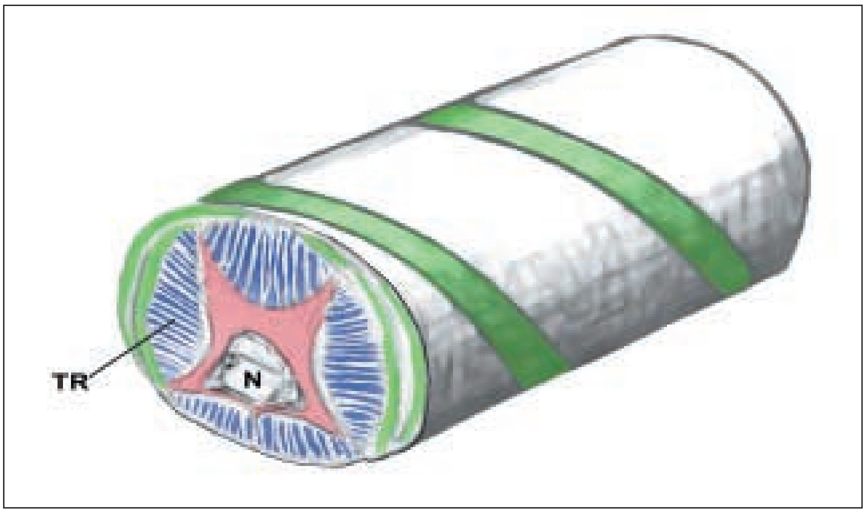

Figure 1. Transverse section of an octopus arm, showing the intrinsic musculature of the arm and the axial nerve cord. The densely packed muscle fibres are arranged in three different groups: transverse muscle fibers (pink) and their trabecular bundles (TR), longitudinal muscles fibres (blue) and oblique muscle fibres (green). The axial nerve cord runs along the center of the arm (N). A schematic diagram shows how one oblique muscle band forms a right-handed helix around the arm (green). Left-handed helix bands are not shown.

A dynamic skeleton

Muscles produce force and pull the skeletal elements. But because muscles can only shorten, a unique arrangement of groups of skeletal muscles that work against each other has evolved. These groups are termed **antagonist muscles** and they are usually connected to the opposing sides of each joint.

But how are the functions of a rigid skeleton performed by a muscular hydrostat? Kier and Smith (1985) have characterised the basic biomechanical principles of muscular hydrostats and described the possible ways in which these structures can change shape and produce movement. Muscular hydrostats have their muscles organised in three main directions: (1) parallel to the long axis (longitudinal muscles), (2) perpendicular to the long axis (transverse muscles) and (3) wrapped obliquely around the long axis (helical or oblique muscles) (Figure 1). When the longitudinal muscles shorten in a certain region of the arm, the whole region shortens but the volume does not change, so that there must be a compensating change in one or more directions different from the long axis. This can be a lengthening of the transverse muscles in the same region, which means that the longitudinal and transverse muscle groups act as antagonist muscles. When all muscle groups are activated together the whole structure stiffens and behaves almost like a rigid element, able to support weight and resist external forces. Other combinations of muscle activations can create a bend in the structure, elongate the organ or twist it around the long axis. Thus, the muscles in a muscular hydrostat act as a dynamic skeleton.

The squid tentacles are an example of muscular hydrostat structures used for prey capture that are especially designed for rapid elongation. A special set of striated transversal muscle fibres contract swiftly and powerfully, squeezing the longitudinal muscles and thus causing the tentacle to elongate (Kier *et al.,* 1997). In this review, we will take the octopus arm as a general model for a muscular hydrostat. Each point along an octopus arm can elongate, shorten, bend and twist; hence. such a structure has a huge number of degrees of freedom. This brings us back to the question of control. How does the octopus use all these degrees of freedom? How is the activation of muscles coordinated? And, finally, what do octopus movements teach us about the control principles of muscular hydrostats?

The reaching movement

Octopuses, being active predators, are intelligent and inquisitive creatures. If a novel object is presented to an octopus in a tank (where it is kept so that we can study it), the octopus usually extends one or more of its arms to grab and inspect the object. Figure 2 shows several frames from a video sequence of such a movement. Gutfreund *et al.* (1996) used such films to analyse these reaching movements in *Octopus vulgaris.* They showed that arm extension is a fundamental component of various behaviours of the Octopus such as locomotion, searching and reaching towards a target; this was the reason they chose this movement for their detailed analysis. A reaching movement is usually composed of the following stages. First, a bend is created somewhere along the arm. This bend is always curved dorsally so that the suckers, located on the ventral side of the arm, point in the direction of movement. The bend then propagates along the arm to the tip, while the proximal part remains extended.

Human and octopus motor systems have evolved along unrelated evolutionary paths. Both species reach towards objects but their arms are completely different. It is thus interesting to compare between their reaching movements to see how nature solved the reaching problem for such different structures.

The path of the human hand towards a target during planar movements in the horizontal plane is roughly straight. In 3D movements, the path is slightly curved. The velocity profiles of reaching in both 2D and 3D movements show a basic invariant bell-shaped curve. The nature of the path and velocity profiles have been used in developing detailed theories about the way the human motor system plans and executes movements (see for example Flash and Hogan, 1985). Humans grab a target with their hand (the end-effector of the system), which is an important controlled variable of the motor system.

The octopus has a different catching tool – its suckers are distributed all along the ventral side of each of its arms and serve as fingers. Therefore, no particular point along the octopus arm can have a role as special as that of the human hand. It is more likely that the **bend-point** position (the point of maximal curvature) is important and thus this may be the part controlled by the octopus motor system.

It is possible to record the movement of an octopus on video and then mark the position of the bend-point as it passes along the arm. Gutfreund *et al.* (1996) quantified

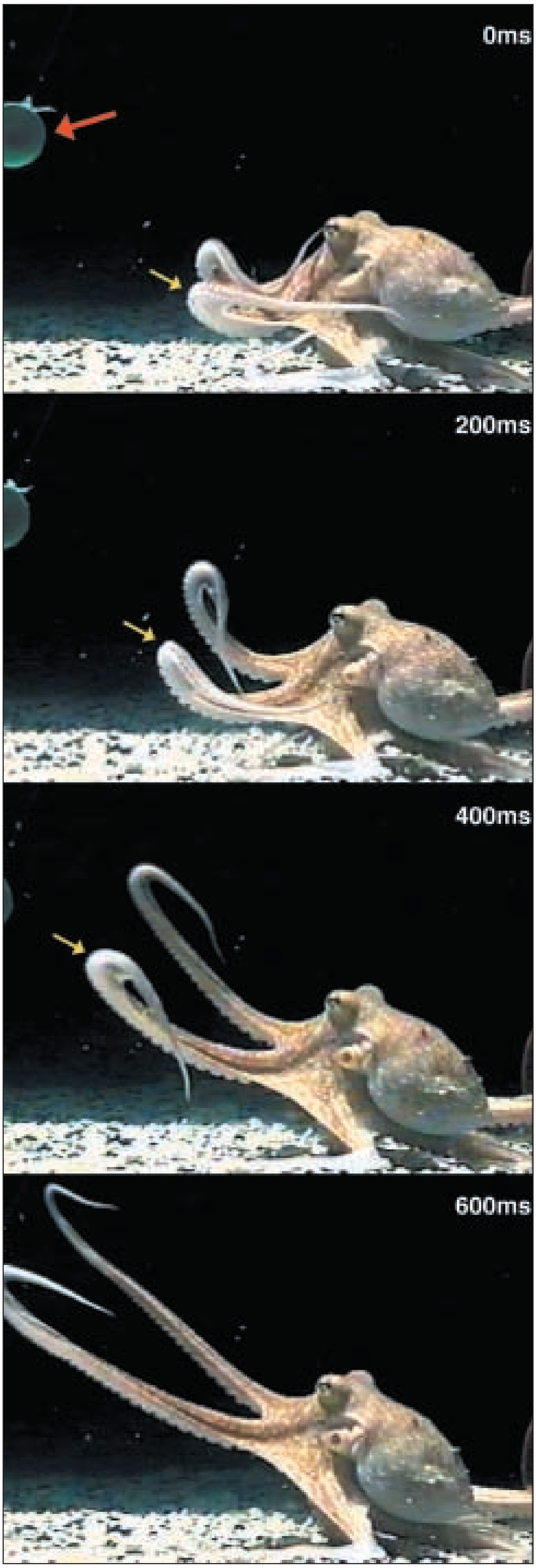

Figure 2. A video sequence of the stereotyped reaching movement. Notice the propagation of the bend point (yellow arrows), and how the part of the arm proximal to the bend remains extended after the bend has passed it. The target is a green disk (red arrow).

the path of the bend-point and showed that it tends to move within a single plane in a simple, slightly curved path. They also looked at the **tangential velocity** of the bend-point (the velocity in the direction of movement), which is characterised by a bell-shaped profile invariant to the direction and duration of movement (Figure 3). Velocity profiles are similar not only in individual animals but also among different animals. When the arm is already extended and a target is presented near the distal part, the octopus usually does not move the whole arm sideways but creates a new bend, pulls the distal part backwards and then uses the stereotyped bend propagation to once again extend the arms toward the target.

If an articulated arm is to be moved towards an object in order to grasp it, all joint angles must be determined such that the arm will fulfil the task. The problem of finding these angles is termed the **inverse kinematics** problem (Hollerbach, 1990). In cases of redundancy (when the manipulator has more degrees of freedom than is minimally needed for a given task), the problem is complicated by the fact that the solution is not unique. The control system must somehow choose one solution from all possible ones and follow this one choice.

It seems that the octopus dramatically reduces the number of degrees of freedom by using a stereotypical reaching movement, which needs a very small number of variables to control it. The base of the arm points at the target and its position can be described by two variables (one angle for the yaw and another angle for the pitch of the arm around its base). One further degree of freedom controls the motion of the bend along the arm. In this way, the inverse kinematics problem is reduced to determining these three parameters only.

EMG and kinematic features of the reaching movement

So far we have described the reaching movement from a **kinematic** point of view, which looks at the position and velocity of the arm during movement. But arm movement is the outcome of arm **dynamics** – the reaction of the arm's mass and inertia to all forces involved in the movement. The octopus nervous system must control the arm muscles to produce appropriate forces, which then create the desired motion.

The problem of determining what muscle forces are needed to follow a desired kinematic plan is termed the **inverse dynamics** problem. Even in 'simple' articulated arms such as the human arm, the inverse kinematics and inverse dynamics problems are not at all trivial. Just imagine the difficulties we face when bringing a hot cup of coffee to our mouth. Our motor control system has to decide upon a kinematic plan that would keep our coffee inside the cup the whole way and then it has to find the correct forces to carry out this kinematic plan.

In a hyper redundant arm, such as the octopus arm, the task of solving the inverse dynamics problem could be alarmingly difficult. But the arm extension movement can serve as a simplifying strategy for the inverse dynamics problem. Gutfreund *et al.* (1998) measured the electrical muscle activity (EMG) of an octopus arm during a reaching movement in order to describe the relation between muscle activity and arm kinematics. They found that a wave of

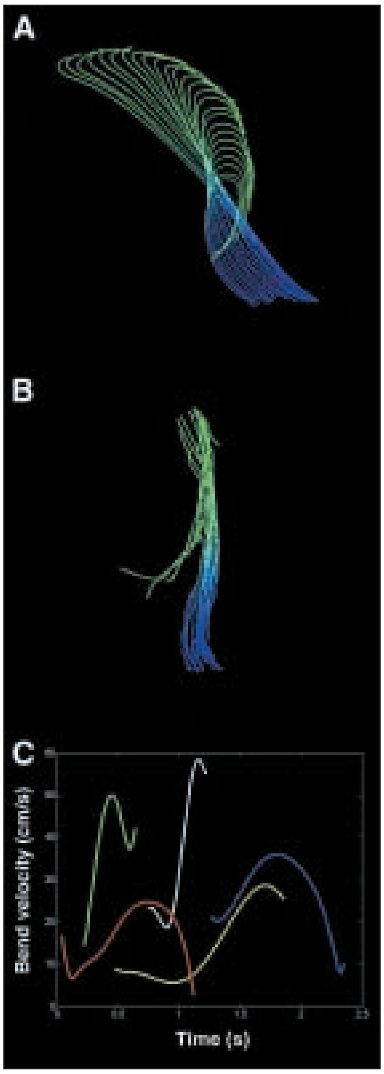

Figure 3. (A) Super-position of a sequence of 3D back-bone curves of an octopus arm (an imaginary line running from the tip to the base along the centre of the arm) during the execution of a reaching movement. The proximal part of the arm is shown in blue and the distal part in green. (B) The same sequence seen from a different point of view. Notice how the movement is restricted to a single plane. (C) Several velocity profiles of the propagation of the bend along the arm. All of them show a characteristic bell-shape profile.

electrical muscle activity moves along the arm and precedes the bend-point. A positive correlation was demonstrated between the amplitude of the EMG signal measured at the beginning of the movement and the velocity of the bend-point measured later. This means that it is possible to predict the kinematic features of the movement using the EMG signal.

The conclusions of this study are that reaching movements are performed by an active process of muscle activity and not by a passive one (like a whip movement). Furthermore, the control of this movement is relatively simple, probably utilising some kind of a feed-forward control mechanism. Gutfreund *et al.* explain that a wave of muscle activation that stiffens the structure and pushes a bend along the arm can account for all measured data. Such an explanation is very appealing from the control point of view. It means that the inverse dynamics are reduced to two relatively simple steps: (1) determining the muscle activity that would orient the base of the arm towards the target, and (2) determining the muscle activity that would stiffen the structure and push the bend forward in a given time.

The extension movement motor program

Looking at the neuroanatomy of the arm, which contains ~5x10^7 nerve cells and only ~30 000 nerve fibres carrying sensory and motor information to and from the brain, it is clear that extensive processing takes place at the level of the nervous system within the arm. Using either electrical stimuli to the axial nerve cord of the arm or mechanical stimuli to the skin, Sumbre *et al.* (2001) succeeded in evoking arm extensions in octopus arms whose nervous system was disconnected from their brain. The kinematic features of the evoked extension movements were similar to those of natural reaching movements (Figure 4). They also showed that the initial posture of the arm determines the direction of the path of an evoked extension movement. All this supports the idea of a division between the central and peripheral levels of the octopus motor control system, resembling the hierarchical organisation found in other invertebrates and vertebrates. It seems that the brain sends global commands to the arm neural network, which is then executed by the neuromuscular system of the arm in an autonomous fashion.

It is tempting to speculate on the nature of the constraints that shaped the evolution of these reaching movement. Looking at the shape of the arm during the

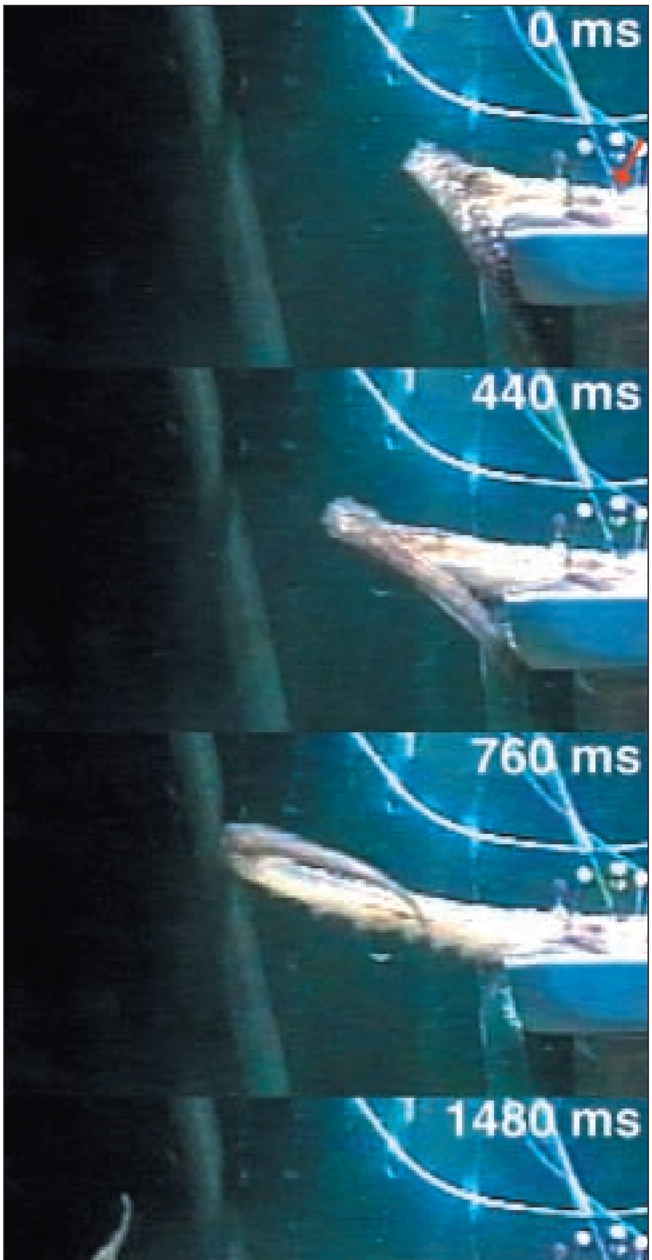

Figure 4. A video sequence of an electrically evoked arm extension movement in a denervated octopus arm. The red arrow shows the position of the stimulating electrode. Notice the similarity between this movement and the movement shown in figure 2.

extension, one is able to estimate the role of water drag forces on the different parts of the arm. It appears that the arm extension movement is an efficient way to move in water, because only a minimal portion of the arm (the bend front) suffers from large drag forces. The arm extension movement can also be the result of minimising the computational complexity of motor control – an important factor to consider when using a hyper redundant arm.

Conclusions and future research

The octopus reaching movement, as described here, is an example of how the octopus motor system elegantly solves the problem of controlling its hyper redundant arm by reducing the number of degrees of freedom. It is important to understand that this reduction is not just choosing some small number of the inherent degrees of freedom of the arm, but combining the degrees of freedom in a way that would not be possible in an articulated arm. Interestingly, the octopus reaching movement is not very accurate, and the octopus seems to be unable to correct movements after their initiation.

Does the octopus have other movement strategies? Our group is actively researching this question. We have just begun a study of the 'fetching movement' – the movement that the octopus uses to bring food to its mouth. While the octopus does not use bend propagation in this behavioural context, it does appear that the Octopus motor system reduces the number of degrees of freedom of the arm in the fetching movement also. However, this reduction is achieved differently for the two types of movements.

The knowledge gained from studying octopus movements may be used in a new generation of octopus-like robots, especially when new materials that can serve as artificial muscles become available.

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Website

www.spike.ls.huji.ac.il/~tamnun

The website of the Octopus Group at the Hebrew University of Jerusalem.

Yoram Yekutieli *is a PhD Student of the Interdisciplinary Center for Neural Computation and the Department of Neurobiology, Institute of Life Sciences, Hebrew University, Jerusalem 91904, Israel.*

yoramkt@cc.huji.ac.il

German Sumbre *is a PhD Student at the Department of Neurobiology, Institute of Life Sciences, Hebrew University, Jerusalem 91904, Israel.*

Professor Tamar Flash *is a Professor at the Department of Computer Science and Applied Mathematics, Weizmann Institute of Science, Rehovot, Israel*

Dr Binyamin Hochner *is a Faculty Member of the Interdisciplinary Center for Neural Computation and a Senior Research Fellow at the Department of Neurobiology, Institute of Life Sciences, Hebrew University, Jerusalem 91904, Israel.*