Motor control of flexible octopus arms

The octopus borrows a jointed-vertebrate strategy to transfer an item between points.

Animals with rigid skeletons can rely on several mechanisms to simplify motor control[1–9] — for example, they have skeletal joints that reduce the number of variables and degrees of freedom that need to be controlled. Here we show that when the octopus uses one of its long and highly flexible arms to transfer an object from one place to another, it employs a vertebrate-like strategy, temporarily reconfiguring its arm into a stiffened, articulated, quasi-jointed structure. This indicates that an articulated limb may provide an optimal solution for achieving precise, point-to-point movements.

Octopuses use their arms to reach a target by generating a stereotypical movement in which only three degrees of freedom are controlled[10–12]. Once the object has been grasped at some point along the arm, the animal needs to execute a point-to-point movement to transfer this object to the mouth. This action of bringing the end-effector (the site on the arm where the object is grasped) to a specific target (the mouth) resembles the execution of motor tasks by articulated arms.

Fetching movements by octopuses (*Octopus vulgaris*) that are allowed to behave freely are most frequently used to bring food towards the mouth (Fig. 1a; for movie, see supplementary information). These are stereotypical movements that were recognizable in roughly 100 filmed trials, and they can be initiated by placing a piece of food anywhere along the arm (for methods, see supplementary information).

The animal's suckers rapidly grasp the food item and a distal and a medial bend form along the arm shortly afterwards; the base of the arm serves as a third (proximal) bend. The locations of the object and of these three bends together define a quasi-articulated structure (Fig. 1a, b), which then rotates mainly about the medial bend in order to bring the distal bend to the base of the arm. Finally, rotation about the distal bend brings the object to the mouth.

Kinematic analysis of the fetching movements (see supplementary information) reveals that the location of the object and the two bends divide the quasi-articulated structure into three segments, each of length L: proximal (L_1), medial (L_2) and distal (L_3) (Fig. 1b). To test whether the bends stay at fixed locations along the arm, we measured each segment length during the execution of the different movements. The slopes of plots of L_1 and L_2 against time did not differ significantly from zero (-0.05 ± 0.14, $P=0.1$; 0.04 ± 0.20, $P=0.07$, respectively, in one-sample *t*-test; data not shown), so L_1 and L_2 must have remained nearly constant. However, L_3 showed a tendency to shorten, with the slope of L_3 against time differing significantly from zero (-0.35 ± 0.26, $P=0.03$; one-sample *t*-test). These results indicate that the bends are behaving like the joints in a skeletal structure.

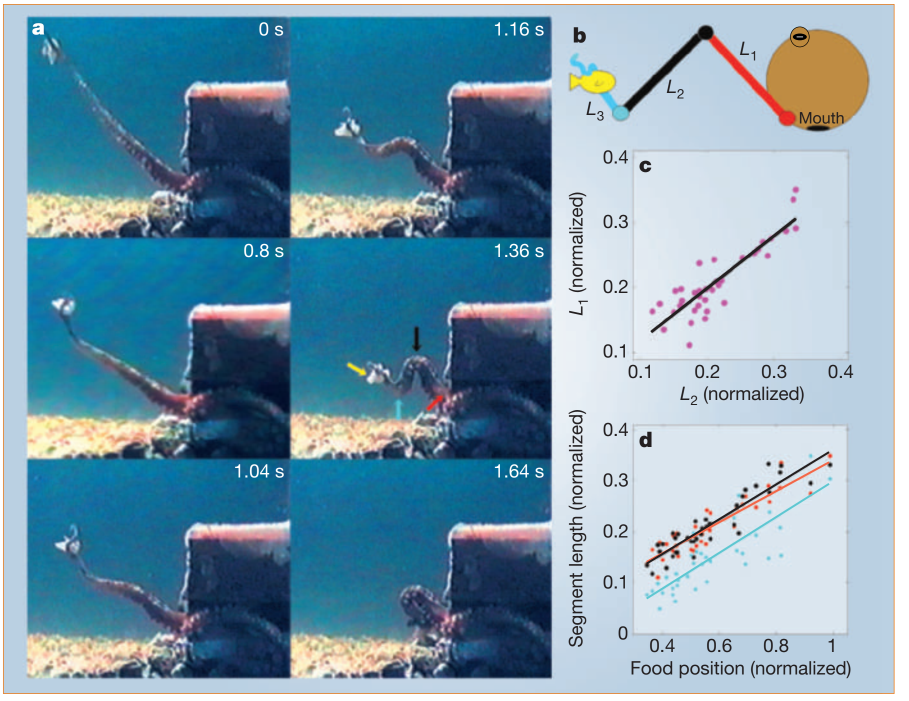

Figure 1 Octopus fetching movements involve a quasi-articulated structure that is based on three bending sites, or 'joints'. **a**, Sequence of video images taken during a fetching movement. Yellow arrow, food item; blue, black and red arrows indicate distal, medial and proximal 'joints', respectively. **b,** Quasi-articulated structure, showing arm-segment nomenclature and coloured as in **a**. **c**, Correlation between the length of the medial and proximal segments ($n=36$); each point represents one trial. **d,** Correlation between the position of the food object along the arm and the different segment lengths (coloured as in **a, b**) ($n=36$). Segment lengths and the position of the food item are normalized with respect to the total length of the arm.

The quasi-articulated structure shows a strikingly invariant geometry for all of the recorded movements (Fig. 1c): L_1 and L_2 are positively correlated (*F*-test, $R^2=0.78$, $P=1.6\times10^{-12}$) with a slope of 0.8 ± 0.15 (mean ± confidence interval). Therefore, during each fetching movement the proximal (L_1) and medial (L_2) segments are almost equal in length, a geometry that resembles the general structure of vertebrate arms and some arthropod appendages.

What is unique to the octopus, and contrasts with the appendages of rigid skeletal animals, is that the segment lengths are positively and linearly correlated with the site on the arm at which the food is grasped (Fig. 1d, and see supplementary information). This result indicates that the configuration of the quasi-articulated structure is dynamically adjusted for each movement according to the position of the grasping site.

Electromyogram recordings made during the fetching process revealed that the quasi-articulated structure is actively contracted, or stiffened, and that the degree of this muscle activity correlates best with the segment lengths (see supplementary information). This finding probably reflects an underlying control strategy for stabilizing the structure against water-drag forces.

It is surprising, given the large number of possible ways in which a flexible arm could convey an object to the mouth, that the octopus uses a quasi-articulated structure that resembles the multijointed, articulated limbs of animals with rigid skeletons. Fetching seems to be an example of evolutionary selection of solutions that are similar even though they are based on quite different mechanisms — on morphology in arthropod and vertebrate limbs, and on stereotypical motor control in the octopus. This functional convergence suggests that a kinematically constrained, articulated limb with two segments of almost equal length is the optimal design for accurately moving an object from one point to another.

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Laser technology

Source of coherent kiloelectronvolt X-rays

Generating X-rays that have the properties of laser light has been a long-standing goal for experimental science. Here we describe the emission of highly collimated, spatially coherent X-rays, at a wavelength of about 1 nanometre and at photon energies extending to 1.3 kiloelectronvolts, from atoms that have been ionized by a 5-femtosecond laser pulse. This means that a laboratory source of laser-like, kiloelectronvolt X-rays, which will operate on timescales relevant to many chemical, biological and materials problems, is now within reach.

High-order harmonic generation in an atomic gas ionized by a femtosecond laser pulse has been successful in generating coherent extreme-ultraviolet radiation[1,2]. The coherent laser field forces the atoms to radiate waves that oscillate in the same way in a macroscopic volume, resulting in the coherent build-up of extreme-ultraviolet radiation in a collimated laser-like beam. The freed electrons cause the generating laser wave and emerging short-wavelength radiation to travel at different speeds and hence limit the useful interaction length, over which the atomic dipoles radiate in phase. Suppression of this de-phasing effect by suddenly turning on the laser field[3], or by modulating the propagation constant in the generation medium[4], results in an extension of harmonic emission to several hundred electronvolts.

We advanced the former approach[3] by pushing ultrafast laser technology to extend the spectral range of coherent radiation to the kiloelectronvolt regime. A multistage titanium:sapphire laser[5] delivers near-infrared pulses of under 15 fs, which are spectrally broadened in a neon-gas-filled capillary and compressed by chirped mirrors in order to obtain 720-nm, 5-fs, 0.2-terawatt pulses at a repetition rate of 1 kHz. The linearly polarized pulses propagate through a 0.4-mm-thick jet of helium atoms (pressure, 0.5 bar; $1/e^2$ diameter of laser beam, $w_0 = 30$ μm). The short-wavelength radiation emerges from the gas jet in a laser-like beam.

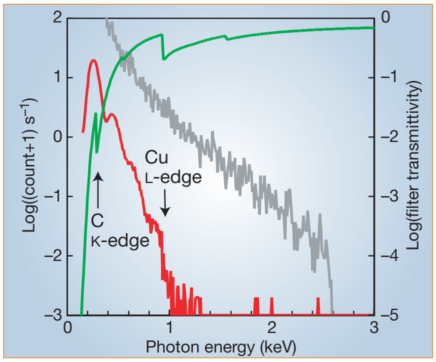

Figure 1 Photon energy spectrum of coherent soft-X-ray emission from a helium gas (red line), measured using a multichannel analyser (Oxford) and a silicon–lithium semiconductor detector cooled by liquid nitrogen. The soft X-ray beam is filtered by propagation through 100-cm helium (3 millibar), 100-nm copper and 100-nm aluminium filters and a 300-nm AP1.3 window (including carbon). Green line, overall transmittivity of these filters; grey line, calculated spectrum of radiation emitted by individual helium atoms exposed to 5-fs pulses with a peak intensity of 1.4×10^{16} W cm^{-2}.

We analysed the beam's spectral distribution using energy-dispersive and wavelength-dispersive X-ray spectrometers, which separate different spectral components according to their photon energy or wavelength, respectively. The combination of aluminium, carbon and copper filters with the helium background atmosphere in the vacuum system blocks light that has photon energies below 200 eV before detection (for methods, see supplementary information). From a knife-edge scan across the X-ray beam, we evaluated a beam-divergence angle of 0.2 milliradians for the spectral range above 200 eV . This divergence implies perfect coherence of the atomic dipoles within a macroscopic volume of diameter of ⩾ 13 μm and ⩾ 4 μm at photon energies of 0.3 keV and 1 keV, respectively. The emitted X-ray beam seems to be diffraction-limited to within a factor of five (see supplementary information).

Figure 1 shows the spectrum of the generated radiation, as transmitted through the filters and recorded with the energy-dispersive X-ray spectrograph. The appearance of the copper L-edge at about 950 eV is evidence for harmonic radiation at 1 keV. X-rays were detected beyond 1.3 keV (see supplementary information). The key to this progress is the temporal intensity gradient in the driving pulse, which allows some 25% of the helium atoms to be ionized within half a cycle before the pulse peak[6]. The electrons detached within this time are pushed in the most intense half-cycle back to the atomic core. Under these conditions, our simulations[6,7] predict harmonic emission from individual helium atoms up to 2.5 keV (Fig. 1).

We have shown that atoms ionized within a few femtoseconds emit coherent, kiloelectronvolt soft X-rays. As the few-cycle pulse can propagate free of substantial distortion over distances that are several orders of magnitude greater than the de-phasing length in the 1–2 keV spectral range, phase-matching techniques hold promise for increasing the current kiloelectronvolt photon flux of 10^2–10^3 photons per second (which is within 10% bandwidth at 1 keV) by several orders of magnitude. Radiation within this band is expected to emerge in a single pulse of less than 100 attoseconds when generated with a waveform-controlled, few-cycle pulse[8]. This would allow the investigation of a wide range of electronic dynamics in atoms, molecules and solids with near-atomic-scale resolution in time, and possibly simultaneously in space[9].

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