The embodied organization of arms coordination in Octopus locomotion

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The rich behavior of octopuses is an inspiring biological example for motor control in soft-bodied animal. The flexible hyper-redundant arms of the octopus endow it with high maneuvering capabilities but also place a great burden on the control system. The main difficulty lies in the need to overcome the problems in interfacing between the sensory and motor information. This is difficult because representation of sensory and motor information in body part coordinates, as in our motor and sensory cortices, is impractical in the octopus as it would need a practically infinite number of representing parameters. Here we present results strongly suggesting that octopus motor control overcame this difficulty by coevolution of a unique body morphology together with unique neuronal and muscular properties. These have led to the emergence of special motor-control strategies that reduce the need to rely on body part representations.

This concept started to emerge during the investigation of the control of goal-directed arm movements, like reaching toward a target and fetching food to the mouth. The control strategies of these movements are drastically simplified by using stereotypical motor programs requiring central control of only few DOFs (Gutfreund et al., 1996, Sumbre et al., 2005). Because the motor programs for these goal-directed movements are embedded in the neuromuscular system of the arm (Sumbre et al., 2001, Sumbre et al., 2006) only motor programs are represented in the higher motor centers of the central brain (Zullo et al., 2009).

Now we are analyzing the mechanism of arm coordination during several octopus locomotion maneuvers. Again, the results are surprising, as they indicate the emergence of further unique locomotion control mechanisms. During various forms of locomotion, octopuses keep their head constantly horizontal. Keeping the head in a fixed reference to the external world simplifies the complexity involved in controlling the soft and very flexible arms, reducing the interactions with the world from 3D to virtually 2D. This constraint is also important for arm coordination in locomotion because, as in all cephalopods, octopus arms are connected directly to the head and therefore the arms that interact with the surroundings are responsible for keeping the head horizontal. This suggests that keeping the horizontal head posture, in turn, constrains and simplifies the control of the interactions of the flexible arms with the substrate during the locomotion, as it helps determine the level of stiffening of the interacting arms (one DOF per active arm). Kinematic analysis of octopus crawling, walking, and climbing suggest that all these locomotion maneuvers are controlled by a 'probabilistic' strategy of moment-to-moment recruitment of the acting arms. This contrasts sharply to the more familiar central pattern generator (CPG) mechanisms, which are likely good strategies for locomotion with skeletal appendages that have only few DOFs. The probabilistic control strategy, together with the radial organization of the arms around the body, enables yet another locomotion uniqueness. We found that, in contrast to all bilaterian animals (animals with bilateral body symmetry), the octopus can locomote in any direction (relative to the facing direction) and, as shown for crawling (Levy et al., 2015), at the same time independently control its body facing orientation.

These findings further support the theory that *embodied organization* of behavior has led to the evolution of unique control mechanisms in concert with the evolution of the 'strange' morphology of this soft-bodied animal.

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