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**Armed With Information:**

**Cognition and Consciousness and the**

**Octopus Nervous System**

Sidney Carls-Diamante

A thesis submitted in fulfilment of the requirements for the degree of  
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## Abstract

The octopus is a fascinating organism which challenges common assumptions regarding the correlation between the nervous system and the mind, especially with regards to the structures of cognition and consciousness. The cognitive and behavioural capacities of octopuses are highly sophisticated and similar to those of many vertebrates, despite the significant anatomical and functional differences between octopus and vertebrate nervous systems.

This thesis explores the implications raised by the octopus for a number of issues within the philosophies of mind, cognitive science, and neuroscience. In particular, it demonstrates that the features of the octopus nervous system are such that they preclude plausibly accounting for the animal's psychological characteristics using the standard explanatory tools of mainstream cognitive science. While this thesis takes a theoretical approach to these issues, it also draws extensively on the findings of empirical research on octopuses from neuroscience, psychology, and biology.

The investigation first focuses on *cognition*. Here, the discussions establish the octopus as proof for the ontological diversity of cognitive processes, and proceed to challenge the causal and epistemic frameworks that are widely received in cognitive science. The latter part of the thesis shifts its focus to *consciousness*. This section presupposes that consciousness exists in octopuses, in order to demonstrate that the structure and adaptive functions of consciousness can differ significantly from those attributed to it by mainstream cognitive science.

The overall objective of this project is to show that cognitive science must radically depart from established, vertebrate-based models of cognition if it is to accommodate octopuses, a species-rich invertebrate genus characterized by behavioural and cognitive complexity. The broader significance of addressing the need for new models of cognition lies in expanding the explanatory scope of the cognitive and brain sciences in order to render them more effective at handling forms of intelligence that are unlike those of vertebrates.



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# **PART I**

## **STAGE SETTING**



## **INTRODUCTION:**

### **WHY SPILL INK OVER THE OCTOPUS?**

What special interest does the octopus hold for cognitive science? The facts of octopus cognition challenge common assumptions about the kind of nervous system needed to support advanced intelligence, especially with regards to the control of flexible, goal-directed actions. The octopus exhibits a versatile repertoire of adaptive behaviour subserved by sophisticated cognitive capacities that are typically associated with vertebrates due to the integration of their nervous systems. This is surprising and almost paradoxical, as the octopus is an invertebrate with a highly distributed nervous system characterized by extensive functional decentralization.

The structural and functional organization of the octopus nervous system gives rise to a type of cognitive architecture that departs significantly from those of vertebrates, with which cognitive science is extensively familiar. That is to say, in octopuses, the set of psychomotor operations responsible for processing sensory input in order to generate adaptive behavioural output differs greatly from its vertebrate counterparts. This divergence from vertebrate cognition is most strongly exhibited in the domain of motor control, rendering the octopus a counterexample to many received and intuitive views on how higher-level or goal-directed actions are produced.

The octopus is an entirely soft-bodied animal, whose lack of a skeleton entails not only the lack of proprioceptive markers by which cognitive routines for controlling and monitoring the movement and posture of the body and its parts can be simplified, but also the absence of the neural mechanisms that are crucial to these functions. This sparseness of proprioceptive information produces another paradox: the more flexible an anatomical structure is, the more difficult it is to control its movements, due to the large number of



spatial parameters to keep track of. That is to say, the octopus's extreme flexibility is such that it would require highly detailed control and monitoring mechanisms—the very ones it does not have. Nevertheless, octopuses are known for being capable of precise and fine movements, which are subserved by a motor control schema peculiar to the kind of neurocognitive architecture the octopus is equipped with.

In addition to its extensive implications for cognitive motor control, the octopus nervous system also raises questions about another psychological phenomenon: *consciousness*, in the sense of persisting subjective or qualitative experience. Within the cognitive and especially the brain sciences, there remains considerable hesitance to regard consciousness in general as genuinely causally efficacious, and subsequently to posit it as a legitimate explanatory tool. Nevertheless, the circles within these disciplines that *are* friendly to the notion of consciousness accept the octopus as being endowed with this particular form of mental life, on the basis of its possession of the “neuroanatomical, neurochemical, and neurophysiological” (Low 2012) features deemed necessary to generate conscious experience. From the three neurological criteria, it can be inferred that consciousness has a substantive causal dependence on its neural substrates. In particular, such a relationship would likely have neuroanatomy determining *which* components of the nervous system contribute to generating consciousness, neurophysiology determining *how* these components contribute to consciousness, and neurochemistry determining the *types* of conscious states that can arise.

In the case of the octopus, the issue of consciousness is not so much one of neurochemistry but one of neuroanatomy and neurophysiology, as it is the latter two that diverge significantly from those of vertebrates and, hence, from familiar models of mental life. That is to say, the question that arises is one of how the distinctive organization of the octopus nervous system will influence its subjective experience, and not of the types of conscious states it can experience. In particular, consciousness in the octopus is likely to differ from what its vertebrate counterparts are believed to be like in terms of structure, i.e., the temporal aspects and relationship between the content of conscious states, as well as function, i.e., how it interacts with the other elements of the neurocognitive system.

Due to its anatomical and physiological features, the neurocognitive system of the octopus is resistant to straightforward explanation by familiar, vertebrate-based models of cognition. What this thesis thus aims to accomplish is to demonstrate how the octopus departs from a number of models, explanatory tools, and received views in the cognitive

and brain sciences, especially with regards to motor control. In doing so, the conclusions it draws can help to expand and update theoretical approaches to the study of the brain and mind in order to render them more effective and efficient at accounting for cognition in the many forms in which it can be instantiated in biological organisms. By eliminating or at least reducing vertebrate bias, cognitive science can be made more flexible and pluralistic when it comes to identifying the necessary physiological conditions of genuine or complex cognition.

While the implications of the octopus for the cognitive and brain sciences and the philosophies of these disciplines are vast, the issues that have been selected for exploration in this thesis are those on which the octopus has the strongest bearing. In particular, the topics that are investigated here are those that have a considerable motor control aspect. As a result, some prominent views on research programs in cognitive science or the philosophy of mind will not be touched on. In the same vein, because this thesis explores how the novelty of empirical findings on octopus cognition and behaviour affects established theories and received views on our understanding of the mind and its workings, it is more “forward-directed” than history-oriented.

As there are not many philosophers who conduct extensive research on octopuses, it is worth noting how this thesis differs from the work that does exist. The most prominent investigations into the mind of the octopus are those of Peter Godfrey-Smith. Godfrey-Smith presents the octopus as a case study in the evolution of cognition, in particular to demonstrate “another way of being a sentient organism” (Godfrey-Smith 2013, 4). His research uses the octopus as a point of reference for tracing the evolutionary history and cladistic distribution of complex cognition. In contrast, the subject matter of this thesis focuses less on the evolutionary origin of mind and cognition, and instead on establishing how the octopus can contribute to understanding the mechanics and processes constituting modern forms of sophisticated cognition.

Much like its object of study, the organization of this research departs from the structure typical of doctoral theses. Rather than monolithically arguing toward a single set of interrelated conclusions, each chapter investigates a self-standing issue in the philosophies of cognitive science and neuroscience for which the octopus raises important points to consider, organised around two central themes: the nature of cognition and the nature of consciousness.

The thesis divides into three parts. The first part is comprised of this Introduction and a chapter that details the evolutionary history, neuroanatomy, and life strategies of the octopus. The second part, consisting of Chapters 3 to 5, is dedicated to investigating how the octopus challenges or calls into question received views on the nature of cognition and the explanatory frameworks used to account for the mechanisms and processes constituting cognition. Chapter 3 establishes how the octopus instantiates three major ways in which cognition is *embodied*. Chapter 4 argues that, although it has embodied components, octopus cognition also employs *representations*, and probes the nature of these representations. Together, these two chapters demonstrate that octopus cognition is an embodied-representational hybrid, and thus necessitates a pluralistic approach to cognition that can reflect this ontological diversity. Closing Part II, Chapter 5 argues that maintaining the traditional notion of the *agent* as the causal locus of cognitive activity is rendered highly problematic when applied to an analysis of octopus cognition.

A conspicuous absence from Part II—which must be singled out as it pertains to a major development in research into the mind—is that of *connectionism*. Because the topics of *classical computationalism* and representations are explored in the thesis, it may come as a surprise that there is no mention of connectionism. The rationale behind this particular exclusion is that the salient points of connectionist approaches to computationalism overlap with other issues discussed in detail. In particular, the connectionist notion of *neural nets* strongly resembles that of the *neural representations* discussed in Chapter 4, while its fluid construal of information processing is likewise captured by the *dynamical approach* to cognition that is explored throughout Chapters 3 and 4. Thus, connectionism is not discussed as an independent theory, as its principles have been absorbed by portions of the investigation into other views.

Finally, the last two chapters of the thesis make up Part III, which investigates consciousness. As consciousness attribution—especially to the octopus—is a fraught issue that requires a separate investigation, a conditional approach will be taken throughout the discussions here. The motivating question for this latter part of the thesis can be articulated as such: “If the octopus were indeed conscious, what would its consciousness be like?” Chapter 6 demonstrates how the established claim that the normal or default structure of consciousness is one that is unified is unlikely to hold in the octopus. Finally, Chapter 7 raises reasons to believe that octopus consciousness may not exhibit the same adaptive functions attributed to consciousness in general.

## THE OCTOPUS

This chapter surveys the biological, neurological, and behavioural features of the octopus that render it a highly interesting creature. It begins with an exposition of the evolutionary history of cephalopods, the class of molluscs to which octopuses belong. The discussion then narrows down to the octopus. After presenting a description of the anatomical and physiological features of its nervous system, it moves on to an overview of its behavioural, survival, and reproductive strategies.

### 2.1 Evolutionary history of cephalopods

Many of the noteworthy cognitive features of cephalopods arose as consequences of their morphological and phenotypic evolution. As such, to best appreciate cephalopod cognition, it must be examined against the backdrop of their evolutionary history.

Cephalopods are an ancient molluscan group that emerged several millions of years before vertebrates (Packard 1972). They first appeared in the Upper Cambrian period, sometime between 510 and 450 million years ago (Hanlon and Messenger 1996; Boyle and Rodhouse 2005). The ancestral cephalopod would have been a mollusc encased in a heavy external shell segmented into gas-filled chambers, affording a capacity for neutral buoyancy. Although buoyancy allowed only a limited form of mobility, it released the ancestral mollusc from the confines of the sea floor, setting the stage for species diversification (Boyle and Rodhouse 2005). Today, the only surviving genus of cephalopods that has retained the ancestral externally-shelled or *echtococleate* body plan is that of the nautilus (*Nautilus*).

While the buoyancy-dependent locomotion of early cephalopods made them more mobile than molluscs of other classes, it was still a restricted form of movement that rendered them vulnerable to predators. These predation pressures were instrumental to the

emergence of the modern groups: the *coleoids* (Coleoidea). Coleoids were, and still are, radically unlike their predecessors in terms of mobility and morphology. In addition to being actively mobile, coleoids depart from the ancestral ectocochleate body plan in a number of prominent ways: the internalization of the shell (where it is not altogether lost), the development of mechanisms for jet-propelled swimming, and the formation of eight or ten flexible appendages, the distinguishing feature of the class. It is thought that coleoids emerged in the Devonian period, with the proposed dates being pegged between 370 to 100 million years ago (Hanlon and Messenger 1996; Boyle and Rodhouse 2005).

Two theories regarding the emergence of coleoids have been offered. In what is known in the literature as the *Packard scenario*, Andrew Packard (1972) hypothesized that the early vertebrates of the Mesozoic (252 to 66 million years ago) preyed extensively on then-ectocochleate cephalopods, forcing them away from their coastal habitats into deeper waters. The physical stress exerted on the shell by the high water pressure of the open ocean led to its minimization, until it was eventually internalized. The reduction of the shell thereby diminished early cephalopods' capacity for buoyancy, and brought about changes to their morphology that provided other means of locomotion. One such morphological modification was the furcation of the ancestral foot into eight muscular arms, affording more possibilities for active mobility. Now in coleoid form, the cephalopods returned to coastal waters, where their increased mobility allowed them to successfully compete with *teleosts*, or bony fish.

In a modification of the Packard scenario—the received view of cephalopod evolution—Richard Aronson (1991) proposed that both ectocochleate and *endocochleate* (internally shelled) cephalopods co-existed within the same habitat, but the less mobile, shallow water ectocochleates were unable to withstand predation pressures brought about by the radiation of vertebrates into diverse species. Regardless of this disagreement, there is consensus that coleoid evolution was heavily influenced by teleosts, with which cephalopods continue to share the same ecological niche.

Extensive speciation of both teleosts and coleoids took place over the last 63 million years, during the Tertiary period (Boyle and Rodhouse 2005), and coleoids display numerous features that evolved in convergence with those of teleosts. In particular, coleoids' ecological strategies, visual system, and behavioural capacities are closer to those of teleosts than to those of other molluscs (Hanlon and Messenger 1996). Likewise, the development of the impressive perceptual and motor systems of coleoids was impelled by the need to remain on a par with their vertebrate competitors. Indeed, the wide geographical

distribution and high species diversity of coleoids is testament to their biological success: they are present in all oceans, from polar to tropical regions. There are about 650-700 coleoid species that have been identified, most of them *neritic* or coastal (Boyle and Rodhouse 2005).

The modern cephalopod class is divided into the subclasses of *nautiloids* (Nautiloidea)—which alone retain the ancestral shell—and coleoids (Coleoidea). Living coleoids (Neocoleoidea) are categorized mainly into cuttlefishes (Sepioidea), squids (Teuthoidea), and octopuses (Octopoda) (Voss 1977). The vampire squid (*Vampyroteuthis*), the single species within its own order (Vampyromorphida), has been identified as the nearest relative of octopuses on the basis of molecular evidence (Boyle and Rodhouse 2005). Due to similarities in their morphology and neurophysiology, the vampire squid is also thought to bear the closest resemblance to an ancestral coleoid from which octopuses descended (Boyle and Rodhouse 2005). Its interesting, not to mention comical, name derives from its rather ghastly appearance: among other features, it has skin that ranges from dark purple to black, spiked suckers, and a wide arm web that resembles an umbrella when spread (Boyle and Rodhouse 2005).

Coleoids are highly intelligent and behaviourally sophisticated due to their complex nervous systems. However, the vertebrate-like behaviour and cognition of octopuses, something that is evidenced by their competence in learning and memory tasks that are usually mastered by vertebrates, has been attributed to their brain structure, which exhibits considerable difference from those of other coleoids (Packard 1972; Godfrey-Smith 2013). (This will be discussed in further detail later in the chapter.) Due to the marked differences in life strategies and behaviour of nautiloids and coleoids, cephalopod studies focusing on one class often exclude the other (Hanlon and Messenger 1996). As this thesis is devoted to the octopus, the term “cephalopod” will be used exclusively to refer to coleoids.

## **2.2 Modern cephalopods**

The general body plan of cephalopods is constituted by a head, mantle, and eight or ten flexible appendages (Boyle and Rodhouse 2005). They have a single pair of gills, and a funnel used for expelling water jets. As mentioned earlier, the ancestral shell has been internalized and significantly reduced. With the exception of a few species, cuttlefish and squids alike have eight *arms* and two *tentacles*, the latter being specialized appendages used exclusively for grasping prey and bringing food to the mouth. In cuttlefish, the shell is

broad and flat, and has retained some buoyancy functions. In long and narrow squids, the shell has been reduced to a thin, non-buoyant structure known as the *pen* or *gladius*. Due to their having ten limbs, cuttlefish and squids are collectively referred to as *decapods*, in contrast to eight-limbed *octopods* in which tentacles are absent. Octopuses, on the other hand, have a distinctive body plan: their heads are fused with the mantle, with a web formed by the bases of their eight arms. All that remains of the ancestral shell is a vestigial pair of cartilaginous rods between the eyes, thus making the octopus almost entirely soft-bodied (Boyle and Rodhouse 2005; Hanlon and Messenger 1996).

The almost complete loss of the ancestral shell was an instrumental factor in octopuses' evolving to become the most cognitively complex group of cephalopods (Packard 1972; Grasso and Basil 2009; Vitti 2013). The elimination of the shell entailed the loss of buoyancy mechanisms, forcing the octopus to adopt a *benthic*, or sea floor, habitat. The rich landscape and diverse ecology of the sea floor confronted the octopus with various physical features and a wide range of species to keep track of, thus requiring it to develop an unprecedentedly wide repertoire of hunting and survival strategies (Godfrey-Smith 2013). The visual systems of octopuses and vertebrates evolved convergently to have the same degree of sophistication, as they were confronted with the same environmental pressures afforded by the visual complexity of the sea floor. The consequential increase in the amount and complexity of visual input in turn necessitated a parallel increase in neurons to keep up with processing demands; the hefty cognitive demands brought about by maintaining a repertoire of varied hunting strategies can be met only if the underlying neural structures are sophisticated enough to support them (Vitti 2013).

The present features of the octopus nervous system are consequences of the radical modifications it underwent due to the rigorous cognitive demands it faced, as well as the evolution of its body plan toward its modern form. The structure of the octopus brain was brought about by the fusion of ganglia into lobes—which retained the molluscan characteristic of being arranged around the oesophagus—as a result of the shortening of the fibres connecting them (Borrelli and Fiorito 2008). This new, compact arrangement facilitated the development in the octopus of cognitive capacities that recruit multiple brain areas, thereby setting the stage for sophisticated cognition (Vitti 2013). New neural structures also developed, forming the peripheral ganglia that would become the arm nervous system (Borrelli and Fiorito 2008), which is of particular interest and centrality to this thesis.

### 2.3 The octopus nervous system

The cephalopod nervous system is the largest and most sophisticated, not just of molluscs, but of all invertebrates (Borrelli and Fiorito 2008; Boyle 1986; Hanlon and Messenger 1996). Although cephalopod nervous systems retain certain neuroanatomical features characteristic of invertebrate nervous systems, they exhibit a considerable degree of anatomical centralization, and have about 200 to 10,000 times more neurons than other invertebrate species (Packard 1972; Borrelli and Fiorito 2008). While most of the lobes of the cephalopod brain evolved from the fusion of ancestral ganglia, others are more recent developments that emerged after cephalopods radiated from the molluscan clade (Borrelli and Fiorito 2008). Among these novel neural structures that evolved uniquely in cephalopods were motor and receptor centres that endowed them with behavioural versatility unprecedented in molluscs (Young 1971).

While cephalopods share a general neuroanatomy, there are some variations across subclasses that are correlated with their respective lifestyles and life strategies. One prominent distinction is octopuses' lack of a giant axon system, a highly-developed neural mechanism found mainly in squids, which allows visual or tactile signals to directly initiate rapid jet-propelled swimming (Hanlon and Messenger 1996). On the other hand, squid and cuttlefish lack sub-frontal and inferior frontal lobes, which are memory stores for sensory—especially tactile—information, and so have significantly less memory capacities than octopuses do (Hanlon and Messenger 1996).

The size of the octopus nervous system, relativized to its body weight, falls within the range of vertebrates: comprised of roughly 500 million neurons—the same number as those in a dog brain—it is by comparison smaller than the nervous systems of birds and mammals, and larger than those of fish and reptiles (Hochner 2004; Hochner 2012; Borrelli and Fiorito 2008). Morphologically, the octopus nervous system is divided into three distinct anatomical components: the central *brain*, the paired *optic lobes*, and the peripheral *arm nervous system*. Significantly, two-thirds of the neurons of the octopus are found in the arm nervous system; i.e., about 350 million neurons distributed between the eight arms. In contrast, the two optic lobes have between 120-180 million neurons between them, while the central brain has only 40-45 million neurons (Young 1971; Hochner 2004). The brain is responsible for high-level coordination and integration functions, the optic lobes process visual input, and the arm nervous system takes on extensive sensory processing and motor control responsibilities (Hochner 2012).



The peripheral components, i.e., the optic lobes and the arm nervous system, have a considerable degree of autonomy; neuroanatomical evidence indicates that the sensory and motor information they send to the brain first undergoes extensive local processing (Hochner 2012). The arm nervous system is exceptionally notable due to the autonomy of its information processing and motor control operations. For instance, an octopus arm that has been amputated or neurally disconnected from the brain can still respond to stimulation the way it would had it been intact (Rowell 1963). Further underscoring the autonomy of peripheral motor control, it has been discovered that the motor centres of the octopus brain are not capable of *somatotopic representation* (point-for-point mapping of the body), posing a puzzle for motor control due to the lack of a central mechanism to monitor the arms (Zullo et al. 2009). As a unique evolutionary development in motor control, the details of motor programs are encoded within the octopus's arms, instead of in the brain where they would be expected to be found (Sumbre et al. 2001). The significant conclusion that all of these findings point to is that, in an octopus, processing and control operations that in vertebrates are carried out by the central nervous system are performed within the peripheral arm nervous system (Hochner 2012).

### 2.3.1 *The brain*

The octopus brain is a decision-making centre that integrates information from the different components of the nervous system. It also issues high-level global motor commands pertaining to the selection of motor patterns, the speed at which the movement is to take place, and orientation toward the general direction of a stimulus (Hochner 2013; Hochner 2004; Zullo et al. 2009).

The octopus brain is connected to the other two components of the nervous system by only about 30,000 fibres—a meagre number, considering that the octopus has 500 million neurons (Yekutieli et al. 2002). In line with the fact that the optic lobes and the arm nervous system each have substantially more neurons than the brain, this scarcity of connective fibres is regarded as further evidence for the comprehensiveness of peripheral information processing (Hochner 2012). It is also consistent with the hypothesis that what are likely to be represented in the motor centres of the octopus brain are motor programs, and not body parts, which come with heavier neural requirements (Zullo et al. 2009; Hochner 2012).

It was discovered early on, on the basis of behavioural and neuroanatomical evidence, that the brain does not receive information about the stretch of the arm muscles

(Graziadei 1971). In more recent studies, stimulation throughout the higher motor centres of the brain elicited the extension of multiple adjacent arms rather than a single one, implying that central motor commands are transmitted to several arms at a time (Zullo et al. 2009). Selection of which arm to activate takes place at the level of peripheral motor centres, as a result of filtering and complementary information provided by local sensorimotor feedback from individual arms (Zullo et al. 2009; Hochner 2012; Richter, Hochner, and Kuba 2015).

Cephalopod brains are unique among molluscs in that the ganglia of their brains are concentrated and clustered into lobes. As cephalopod brains are arranged around the oesophagus, their main anatomical divisions are named according to their position in relation to it: the *supraoesophageal mass* above, and the *suboesophageal mass* below.

The lobes constituting the supraoesophageal mass are responsible for behaviour, motor control, and coordination, and for processing visual and tactile information (Boyle 1986; Young 1971; Borrelli and Fiorito 2008). Among them are the *basal lobe system*, the *inferior frontal lobe system*, and the *vertical lobe system* (Hanlon and Messenger 1996; Boyle 1986). These lobes are higher motor centres that are responsible for coordinated movement, with the basal lobe system being especially important. Controlled by the optic lobes, it carries the primary control responsibilities over the lower and intermediate motor centres (Hanlon and Messenger 1996). The inferior frontal lobe system is a tactile memory centre, and is responsible for processing chemo-tactile information used in controlling movements such as bringing food objects to the mouth (Boyle 1986). The vertical lobe system, which is the highest processing centre in the octopus brain and is similar to vertebrate memory systems, is a visual memory centre that plays a vital role in learning visual discriminations (Packard 1972). Together with the superior frontal lobes, the vertical lobe system regulates attack and retreat behaviour. Meanwhile, the lobes of the suboesophageal mass are lower or intermediate motor centres responsible for innervating and controlling the effectors, e.g., the arms, eyes, and head (Boyle 1986). The supraoesophageal and suboesophageal masses are connected by the *magnocellular lobes* that encircle the oesophagus (Hanlon and Messenger 1996). In octopods, they are responsible for activating defensive reactions that involve the entire body (Young 1971).

### 2.3.2 *The optic lobes*

In addition to processing visual information, the optic lobes are also memory storage centres with high-level motor control responsibilities. They are arranged bilaterally, with

one for either eye. Octopus vision is *lateralized*, with each eye receiving different and sometimes conflicting information (Messenger 1971; Byrne, Kuba, and Griebel 2002). With all elements on the same side, the eye projects to the optic lobe, which in turn sends motor commands based on retinal information to the basal lobe (a high-level motor centre). Visual information is also transmitted to the intermediate and lower motor centres, via connections to the magnocellular and peduncle lobes, the latter of which are involved in motor control, and defensive strategies such as changing colours and inking (Hanlon and Messenger 1996; Boyle 1986). As a consequence of lateralization, information transfer from one eye to another is not automatic: a visual discrimination task learned with one eye has to be learned anew by the other (Mather 2008). To avoid incoherent behaviour brought about by conflicting visual information, visually directed motor commands must be synthesized. This consolidation is believed to take place in the peduncle lobes, which use visual information to control locomotion (Messenger 1971).

The optic lobes are also involved in controlling skin patterning: retinal information processed in the optic lobes is sent to the chromatophore lobes, thus activating the *chromatophores*, elements on the skin that are responsible for producing colour patterns and textures. At this point, it must be noted that while chromatophores are neurally controlled, they are also photosensitive; the wavelength of light they are exposed to also influences their activation and thus the colours they display (Ramirez and Oakley 2015).

The highly developed cephalopod visual system evolved in convergence with those of vertebrates, so it is unsurprising that their visual capacities are equipotent (Packard 1972). The resolution of the octopus eye and the sophistication of its visual processing are comparable to those of vertebrates (Michael Kuba, personal communication). Heavily dependent on vision, octopuses are capable of visually discriminating between shapes, orientations, patterns, and degrees of brightness; while they cannot perceive colour, they can distinguish between shades of grey (Boyle and Rodhouse 2005).

### 2.3.3 *The arm nervous system*

The arm nervous system of the octopus is singularly fascinating, due to its functional autonomy and physiological organization. A peripheral component of the nervous system, it has extensive motor control responsibilities that are carried out independently of the brain. The comprehensiveness of peripheral processing significantly reduces the workload for which the brain would otherwise have been responsible (Hochner 2012).

Octopuses use their arms to perform a wide variety of tasks—ranging from locomotion, to object retrieval to exploration, and more—and do so with great precision. In addition to motor functions, the octopus arm nervous system processes chemical, tactile, and mechanical information sourced from numerous receptors in the *suckers*, skin, and muscles; this information is integrated at the level of the individual arm before being transmitted to the brain. Each arm has about 300 suckers arranged in two rows on its underside. Used in grasping, the suckers exert a strong gripping force, and have a reflex tendency to adhere to whatever surface they come into contact with. They are also extremely sensitive to tactile and chemical stimuli.

Octopus arms are dense muscular structures without any hard parts. As such, they have unlimited flexibility and degrees of freedom of movement. Due to their muscularity, octopus arms are also very strong, and are able to match the force of being pulled on by an adult human (Boyle and Rodhouse 2005). In the absence of a skeleton, structural support is provided solely by the arm musculature (Gutfreund et al. 1998; Yekutieli et al. 2002). The intrinsic muscles of the octopus arm are arranged in three groups (longitudinal, transverse, and oblique) oriented perpendicularly to each other. In such an arrangement, known as a *muscular hydrostat*, muscular volume remains constant, so that the distinct groups lengthen and shorten to compensate for each other's stretch. Other examples of hydrostatic structures are vertebrate tongues and elephant trunks (Hochner 2004).

In itself, the availability of countless degrees of freedom to octopus arms is already a motor control challenge due to the potentially unlimited spatial coordinates to keep track of. This challenge is further compounded by the octopus's lack of central interoceptive mechanisms to monitor and guide movement. Without proprioception and somatotopic mapping, information about the stretch and movement of the arms cannot be relativized with respect to the rest of the body. In a unique evolutionary development, motor control in an octopus is simplified through the use of stereotypical motor patterns whose kinematic details are contained within the arms (Sumbre et al. 2001). As arm-based motor control is a recurring subject in this thesis, its various aspects will be examined in greater detail as they arise in the succeeding chapters.

The anatomy of the arm nervous system was discussed in depth by Pasquale Graziadei (1971), in a work that is still considered the most comprehensive and reliable reference on the subject. In each arm are found an *axial nerve cord*, four *intramuscular nerve cords*, and numerous *sucker ganglia*, which provide motor innervation to their respective arm. The axial nerve cord, which is a high-level peripheral processing and

control centre (Richter et al., 2015), interconnects the brain, the arm muscles, and suckers. Functionally, it transmits high-level motor commands from the brain to the respective arm, integrates local sensorimotor input, and consolidates these central and peripheral sources of information. Anatomically, it consists of a chain of ganglia that originate from the brachial lobes of the brain, and run throughout the length of the arm. This ganglionic chain is situated on the inside of a pair of nerve bundles called the *cerebro-brachial tracts*, whose fibres connect different areas of the arm with the brain. Each individual ganglion sends out sensorimotor nerves that innervate either the suckers or the arm muscles, and connective nerves that link the axial nerve cord with the intramuscular nerve cords and sucker ganglia.

Each arm has four intramuscular nerve cords, and as many sucker ganglia as there are suckers. These are all lower nerve centres that also have reflex control functions. The intramuscular nerve cords derive their name from being embedded lengthwise within the arm musculature, whose motor innervation they are responsible for. The sucker ganglia provide motor innervation to the suckers and their stalks, or *peduncles*, and receive input from the suckers' sensory receptors. These small ganglia are arranged along the axial nerve cord facing toward their respective suckers, at whose bases they are located. The number of neurons—which is in the hundreds—within a sucker ganglion depends on the size of the sucker it innervates.

Transfer and integration of information between the arms takes place in the *interbrachial commissure*, a ring of neural fibres that runs around the base of the arms (Mather 2008). It is comprised of two systems: the first connects each arm to the adjacent ones on either side, while the second interconnects all the arms. The commissure also contains fibres from the roots of the axial nerve cords. While individual arms have considerable autonomy when it comes to motor control, an intact commissure is required for activities that involve the coordinated participation of multiple arms, such as walking and handling prey (Boyle 1986).

Additional sensory information is provided by around 240 million sensory receptors distributed among the arms that respond to tactile, mechanical and chemical stimuli. Each sucker has tens of thousands of receptors, which send their information to the sucker ganglia. Other receptors are found on the skin of the arms. Yet others are embedded deep within the arm muscles, recording information about the activation or stretch of the muscles. The receptors in the muscles send their axons to the sucker ganglia and to the intramuscular nerve cords, so that “information regarding the stretch of the muscles does

not reach the learning centres of the brain...[but]...is used in local reflexes only” (Graziadei 1971, 59).

#### *2.3.4 Distribution of labour*

This thesis takes particular interest in how cognitive labour, especially with respect to motor control, is divided between the octopus’s brain and arm nervous system. As has been discussed in earlier sections, motor control responsibilities in the octopus are non-redundantly distributed between the central and peripheral components of its nervous system: high-level global commands transmitted by the brain are supplemented and refined by arm-specific sensory information and motor programs. Indeed, it has been hypothesized that the development of such a control organization led to the elimination of the need for central somatotopic representation (Hochner 2012; Zullo et al. 2009).

The octopus brain has been described as a decision-maker, as it is responsible for selecting and initiating responses to the various stimuli the animal encounters. When the brain receives information from peripheral sources, it issues a global motor command that generates a behavioural response appropriate to the stimulus, and that contains information about the speed at which an action is to be carried out (Sumbre et al. 2001; Hochner 2012). Due to the lack of central somatotopic representation, such motor commands are transmitted to multiple adjacent arms. The selection of which arm or arms is to be used to execute the task is determined at the peripheral level, with the involvement of local sensory information (Zullo et al. 2009; Richter, Hochner, and Kuba 2015).

Empirical findings, among which Rowell (1963) and more recently Sumbre et al. (2001) are prominent, indicate that the motor patterns for stereotypic movements are embedded within the neuromuscular system of the arm, rather than being encoded in the brain. The stimulation experiments of C. H. Fraser Rowell (1963) on amputated or neurally isolated octopus arms demonstrate that the motor responses of the arms and suckers to tactile and electrical stimulation are identical to those exhibited by intact appendages. Similar results achieved by German Sumbre and his colleagues (Sumbre et al. 2001) led to the conclusion that “the arm neuronal networks produce the neuronal activation patterns prescribing all of the spatiotemporal details of the basic movement patterns” (Sumbre et al. 2001, 1848). These findings are consistent with a study led by Letizia Zullo (Zullo et al. 2009), which demonstrates that stimulation to the higher motor centres of the brain produces simultaneous and identical motor responses in multiple arms. What these results indicate is that the representation of the body in the brain is coarse-grained, i.e., not detailed

enough to enable specific control of individual appendages. The conclusions of these experiments support early findings by Graziadei (Graziadei 1964) that demonstrate that information about muscular tension is transmitted only as far as the peripheral ganglia, implying that the brain is not involved in determining the spatial parameters of arm movements.

## 2.4 Displays and crypsis

*Crypsis* refers to the set of techniques an animal uses to disguise itself. While the most familiar type of crypsis is *camouflage*, which involves altering skin colour and texture to match the background, crypsis also subsumes changes to posture and observable patterns of behaviour. Camouflage is an important aspect of cephalopod behaviour that evolved in response to predation pressures. It has been hypothesized that the sophistication of cephalopod crypsis was influenced by the need to be effective against the visual capacities of a diverse range of vertebrates, i.e., fishes, birds, and marine mammals (Mather 2004a).

Even among cephalopods, whose capacities for crypsis are impressive to begin with, octopuses are nonpareil. To camouflage themselves, octopuses produce patterns on their skin, called *displays*, which they also use in other kinds of behaviours, such as defence and communication. These displays are highly accurate and versatile, enabling octopuses to blend into almost any naturally occurring background within milliseconds. While camouflage is the type of cryptic behaviour that is used most frequently by octopuses, it is not the only one: when a better disguise is needed, they also alter their body outline and locomotion techniques to imitate other animals (Norman et al. 2001).

Hanlon and Messenger (1996) present an excellently detailed overview of cephalopod skin displays, which will be summarized here. The colour component of a display is produced by two morphological structures: chromatophores and *reflecting cells*. Chromatophores, which are present all over the octopus's skin, are the main colour elements. They are comprised of a sac containing yellow, red, black, and brown pigments. Contraction of the muscles encircling the sac expands it and exposes the pigments, while relaxation retracts the sac and conceals the pigments. As suggested by their name, reflecting cells reflect light to produce shades of blue, green, and white. There are two types of reflecting cells: *iridophores* and *leucophores*. Iridophores are responsible for producing blue, green, and violet patches, while leucophores—in species that have them—produce white. In addition to colour camouflage, octopuses can also change the texture of their skin

by activating their dermal muscles to form *papillae*, or tiny bulb-like projections of flesh. Since these muscles are also under neural control, formation of papillae is extremely precise, allowing the octopus to mimic the texture of almost every surface against which it finds itself (Hanlon 2007).

Control of the mechanisms underlying skin displays has both central and peripheral components: in addition to direct neural control, mainly from the chromatophore lobes of the brain, these mechanisms are activated also by exposure to light (Ramirez and Oakley 2015). Selection of displays is done on the basis of visual input. Retinal information is first sent to the optic lobes, whose high-level contributions to motor control come in the form of commands necessary for producing an appropriate pattern. This information is then transmitted to the lateral basal lobes, which send it on to the chromatophore lobes, which activate the chromatophores and muscles involved in patterning.

Interestingly, cephalopods are colour-blind, yet are able to match the colours of natural backgrounds accurately. While much of camouflage is achieved through matching the brightness of the background, the fact that pigment is involved in the disguise indicates that it is targeted toward observers that are capable of colour vision, i.e., vertebrates (Mather 2004b). A definitive explanation for how cephalopods are able to produce accurate colour displays in spite of their colour-blindness was recently provided by M. Desmond Ramirez and Todd Oakley (2015). They discovered that cephalopod skin contains *opsins*, a light receptor protein also found in their eyes. When exposed to light, the opsins activate the chromatophores, causing them to expand and display their pigments; this process was termed *light-activated chromatophore expansion*, or *LACE*. In experiments conducted on skin removed from *Octopus bimaculoides*, it was discovered that exposure to white light elicited chromatophore expansion, while red light produced no response. Another finding was that skin from adult octopuses produced more consistent and accurate chromatophore responses to light than skin from hatchlings did. Thus, in addition to visual input and centrally selected patterns, the control of skin displays requires the stimulus-dependent activation of elements on the skin itself.

Displays are used by cephalopods as a form of communication, both between conspecifics and non-conspecifics (Mather 2004a). The complexity of communication varies across the cephalopod class, depending on the life strategies characteristic to the different orders. Being the most social of the cephalopods, squids have the best-developed repertoire of communicative signals. On the other hand, communication is limited in octopuses, most species of which are solitary. Communication in octopuses has two main



purposes: to convey the intention to mate to a female, or to threaten or warn approaching animals to stay away (Michael J. Kuba, personal communication).

Crypsis is the primary defence strategy of octopuses; only if it fails do they use more aggressive defence mechanisms. When threatened or approached by an unfamiliar animal, be it a conspecific or not, they first resort to cryptic behaviour. Cryptic defence in octopuses can be categorized into *background matching*, *countershading*, and *disruptive colouration* (Hanlon and Messenger 1996). In background matching, the octopus camouflages itself to imitate the colour and texture of the surface it comes against, such as coral or rock, or even seaweed. Background matching in octopuses is highly plastic, in contrast to vertebrate camouflage that is generally stereotypic and limited to familiar backgrounds.

Countershading involves pigmenting the skin in such a way as to neutralize shadows, thereby lessening the chance of a predator detecting the octopus's actual body outline. For instance, an octopus swimming against the light will often make the skin on its unilluminated areas paler to compensate for the darkness of the shadow. For countershading to be effective, it must be able to maintain constant lightness or darkness with respect to the angle of illumination, as well as movement. Consistent countershading is made possible due to the participation of the *statocyst* systems, which are involved maintaining postural stability amidst the effects of gravity and acceleration, and in controlling countershading mechanisms (Williamson 1995).

Like countershading, disruptive colouration disguises the octopus's body outline, but does so through deceptive markings that make its body plan look different from what it actually is. One type of disruptive colouration is the use of markings, such as false eye-spots, to divert attention away from important body parts. Some octopus species are even known to duplicate the markings of non-conspecific species in order to deceive observers—and potential predators—into mistaking them for another, less appealing species. Disruptive colouration is frequently combined with rearrangement of the body outline and changes in locomotion patterns, producing a highly sophisticated disguise. One example of such complex crypsis is the aptly named mimic octopus's (*Thaumoctopus mimicus*) imitation of the markings and movements of a flounder when swimming across sand plains (Hanlon 2007).

When cryptic behaviour fails to deceive a predator, the octopus uses defence strategies that include rapid jet-propelled escape, inking—releasing either a cloud of ink or mucus-bound ink blobs to create decoys—jetting water at the intruder, *deimatic* behaviour,

and *protean* behaviour (Hanlon and Messenger 1996). Deimatic behaviour is used to intimidate approaching animals, be they conspecifics or not. A common example of deimatic behaviour is the octopus's turning extremely pale, or blanching, and spreading its arms and arm web, to give it the appearance of being larger. Meanwhile, protean behaviour involves confusing predators by carrying out a series of random and erratic actions. This unpredictability prevents predators from developing formulaic strategies for dealing with octopuses.

## 2.5 Reproduction

Octopuses are short-lived animals that die soon after reproductive maturation. Their life expectancy is usually one or two years, although the giant Pacific octopus (*Enteroctopus dofleini*) has a life span of three to five years (Boyle and Rodhouse 2005). From an evolutionary perspective, the short lifespan of octopuses is paradoxical; animals that are large and cognitively complex are normally long-lived, due to the time required to reach morphological and psychological maturity (Boyle and Rodhouse 2005). Octopuses vary greatly from one ontogenetic stage to another, and mature rapidly. As hatchlings, they are *planktonic* or drifting, and remain so for up to an average of two months, after which they descend to the sea floor and adopt a predatory lifestyle that carries into adulthood.

Unusually for large and highly intelligent animals, most cephalopods are *semelparous*, i.e., female octopuses die after laying eggs just once (Hanlon and Messenger 1996). Males are often eaten by the females immediately after copulation, or die soon after mating due to drastic hormonal changes (Hanlon and Messenger 1996). In male octopuses, the third right arm is anatomically modified to enable the transfer of spermatophores, or sperm-containing packets, to the female. This modification, termed *hectocotylization*, consists of a groove running along the entire arm through which spermatophores pass, and a spoon-like arm tip (Hanlon and Messenger 1996). The hectocotylized arm is inserted into the female's mantle cavity to reach the oviducal gland, into which spermatophores are pumped and stored. Spermatophores are deposited once every several minutes, and mating can take up to two hours. However, in octopuses, mating and fertilization take place separately, allowing a female to mate multiple times before laying eggs. Fertilization occurs when the eggs travel down the oviducal gland and come into contact with the stored spermatophores.

Likely due to their solitary nature, courtship behaviour does not usually occur in octopuses, unlike in squid and cuttlefish. Instead, a male octopus will mate with an approaching female almost immediately. However, male octopuses often put on “*sucker displays*,” in which the arms with exceptionally enlarged suckers—usually the second and third arm pairs—are raised (Packard 1961). Sucker displays may be performed by males to identify their sex to approaching conspecifics, in order to avoid being attacked or cannibalized by larger females (Packard 1961), as well as to prevent being forced into copulation by another male (Wells 1962).

With the exception of a very few species, female octopuses lay eggs only once, and die of starvation almost immediately after they hatch. Fertilization takes place when eggs encounter stored sperm as they make their way down the oviducal gland (Hanlon and Messenger 1996). Over the course of several days, the female deposits about 150,000 eggs, which are laid in strings and attached to the wall of the den (Wells 1962). In species that do not keep dens, females have been observed to carry the eggs around in the arms (Hanlon and Messenger 1996). Brooding, or tending to the eggs, takes place for about six weeks, during which the female flushes water jets at the eggs to keep them clean and aerated. During the entire brooding period, the female neither eats nor leaves the den, or does so very infrequently. Because female octopuses are usually semelparous and die shortly after their eggs hatch, there is little generational overlap in octopuses.

## **2.6 Behaviour**

Another interesting feature of octopuses is the unexpected versatility and sophistication of their behavioural repertoire. This section presents a number of examples of octopus behaviour and psychological capacities that are regarded as cognitively salient, and which are among those that have attracted the attention of theoretical and empirical researchers on the mind and brain. Results of numerous experiments testing various cognitive domains have repeatedly demonstrated that octopus behaviour is more comparable to that of vertebrates than it is to that of any other invertebrate species (Godfrey-Smith 2013). It has been hypothesized that the versatility of octopus behaviour is a consequence of their having evolved alongside a highly diverse range of vertebrates, with whom they had to compete in order to survive (Borrelli and Fiorito 2008).

Octopuses have extensive capacities for both short- and long-term memory, learning, and perceptual processing, the integration of which is responsible for the

sophistication of their behaviour and cognitive capacities (Mather 2008; Hochner, Shomrat, and Fiorito 2006). Long-term memories in an octopus can last for months, which is highly significant given their short life spans (Hanlon and Messenger 1996). An example of octopus behaviour that highlights the involvement of learning and memory is prey handling. When handling unyielding prey, such as bivalves, octopuses use a variety of techniques that they select through trial and error, and do not persevere in using an ineffective technique (Mather 2008). Another example is the variety and unpredictability of avoidance behaviours octopuses use when they are presented with stimuli with which they have had previous unpleasant encounters (Mather 2008).

Like vertebrates—especially mammals—octopuses are capable of associative learning and reversal of learned associations, sensitization and habituation to stimuli, use of multiple cues in visual discrimination, stimulus generalization, spatial learning, and conditional discrimination (Hanlon and Messenger 1996; Hvorecny et al. 2007). They are also able to visually discriminate between orientations, rotations, and mirror images of the same object, strongly suggesting a capacity for concept formation (Mather 2008). Early studies have found that octopuses are also capable of tactile discriminations pertaining to shape, curvature, and striation of an object (Wells 1964; Wells and Wells 1957).

Another type of cognitively interesting behaviour exhibited by octopuses is denning. Many octopus species construct dens, by digging a hole in a soft substrate (usually the sea bed) and using it as a shelter. They have been observed also to gather stones with which they line the opening of the den. Octopuses occupy their dens for extended periods of time, ranging from several days to a few weeks. As predators, octopuses go on hunting trips that last up to several hours and cover significant distances, and return to their dens to eat their prey. Importantly, when leaving and returning to their dens, octopuses use different and unpredictable routes, which they do not retrace (Mather 1991). Denning behaviour in octopuses is suggestive, if not demonstrative, of a number of cognitive capacities. It has been hypothesized that octopuses are able to form, store, and retrieve mental maps of the area around their dens (Hanlon and Messenger 1996), and to use prominent features of the environment as navigational aids (Mather 1991; Hvorecny et al. 2007). The use of visual landmarks has been taken to be indicative of conditional discrimination, an advanced cognitive capacity wherein the context in which an object is embedded is used as a discrimination cue (Hvorecny et al. 2007). In octopus navigation, conditional discrimination involves identifying a particular token landmark as distinct from another

token of the same type by relating it to the surrounding environmental features, or by recognizing the same landmark from different angles (Hvorecny et al. 2007).

Octopuses have a remarkable capacity for recognizing individuals, be they conspecifics or not. This capacity is both unsurprising and unexpected. The highly developed visual acuity of octopuses enables them to detect and discriminate between minute details, making it unsurprising that they are capable of distinguishing between individuals. However, because octopuses are solitary, it is unexpected that they would have such a capacity. In contrast to social species—which usually also exhibit strong dominance hierarchies that necessitate fine-grained individual recognition capacities—octopuses’ solitary lifestyles would not require more than basic social recognition, such as species recognition, or recognition of the sex of conspecifics (Boal 2006). However, octopuses can recognize not only individuals belonging to the same species as they (Tricarico et al. 2011), but also individual human handlers, to whom they respond differently (Anderson et al. 2010). To test the latter, identically dressed individuals would repeatedly approach the octopuses over a period of several days. Some of these individuals consistently offered food to the octopuses, while others consistently applied noxious but harmless stimuli to them. (The octopuses were poked with a brush.) Later on, the same humans would approach the octopuses, but without any stimuli of any sort. The octopuses’ responses were markedly different toward different individuals: they would swim up to those who had given them food, while they would hide from or squirt water jets at those who had irritated them.

It has been said that octopuses exhibit considerable individuality. When kept in captivity, octopuses are initially timid. However, after a few days their natural curiosity re-emerges (Borrelli and Fiorito 2008). As soon as they have adjusted to their new environment, they begin to explore their surroundings, and closely watch whatever comes within their sight, whether it is inside or outside their holding tanks. The adaptability of octopuses to conditions in captivity has allowed researchers to observe distinct personalities in them (Mather and Anderson 1993). Octopuses have also been observed to have individual preferences for particular arms (and eyes), a phenomenon previously thought to be confined to vertebrates (Byrne et al. 2006b; Byrne et al. 2004; Byrne et al. 2002). Arm preference in the octopus is unexpected, as all its arms are capable of performing the same tasks with the same efficiency. While more work needs to be done to investigate the cognitive significance of these individuating characteristics, they are intuitive indicators of octopuses’ psychological complexity. In particular, they point to a

departure from mere stimulus-dependent mechanisms for controlling or producing behaviour.

At least one octopus species has been observed to collect and use discarded coconut shells as portable shelters, which has sometimes been interpreted—although not unambiguously—as tool use (Finn et al. 2009). The octopuses observed were seen carrying either a halved shell, or two halves that they had stacked one on top of the other. These shells were gripped inside the arm web as the octopus walked with its arms on the substrate. To conceal itself, the octopus would either hide under a single shell half (if only one was available), or close the two halves around itself and hold them in place from the inside.

Yet another interesting behaviour observed in octopuses that draws attention to their mental life is their tendency to “play” with objects (Kuba et al. 2006). Octopuses in the lab have been repeatedly observed to blow jets of water at an object to propel it toward the aeration vent of the holding tank, in what has been described as an octopus’s version of bouncing a ball (Kuba et al. 2006). The current from the vent would then drift the object back toward the octopus, which would jet at it again. Genuine play behaviour is highly interesting, as it involves advanced cognitive capacities similar to those indicated by tool use; notably, the ability to form concepts of an object and the ways in which it can be manipulated.

The types of behaviour selected for this survey—which is by no means comprehensive—were chosen because they reflect the cognitive complexity of the octopus. These behaviours recruit the participation of multiple cognitive domains, and demonstrate varying degrees of independence from occurrent stimulation. In other words, they can be used as evidence that octopus behaviour is not merely produced as reactions to environmental conditions or stimuli, but requires the contributions of sophisticated cognitive mechanisms as well.

It is important to note that octopus cognition has been classified as *domain-general* (Vitti 2013). In contrast to *domain-specificity*, wherein the cognitive capacities of an animal are limited to what it needs to survive within its ecological niche, domain-generality enables the animal to respond with versatility to novel situations. Thus, the observable outcome of domain-general cognition is versatile and adaptive behaviour. Significantly, domain-generality is usually found in species with extensive social interaction—such as mammals and birds—due to the cognitive demands imposed by such a lifestyle. It is also associated with centralized nervous systems, as such an organization facilitates the recruitment of the myriad neural mechanisms that subserve complex cognition. Thus, it is

highly unusual for domain-generalty to be found in the octopus, a short-lived, solitary invertebrate with a functionally decentralized nervous system.

# PART II

## COGNITION

The following chapters demonstrate how the octopus departs radically from familiar models of cognition, which for the most part are vertebrate-based. Chapters 3 to 5 collectively establish that cognition in the octopus is comprised of anatomically distinct, functionally autonomous, and ontologically dissimilar elements that contribute non-redundantly to cognitive processing. To be more precise, the format—representation-using, or embodied and dynamical—of a given cognitive routine depends on whether its substrates are localized centrally or peripherally in the octopus nervous system. The discussions focus mainly on motor control, a cognitive domain that is exceptional in the octopus due to its substantial peripheral component.

An established notion challenged by the octopus is that of the cognitive agent. The unique and extensive distribution of neurocognitive labour between the central and peripheral components of the octopus nervous system raises questions about how—and where—cognitive processing is initiated and directed within a single, normal octopus. The possibility of multiple cognitive agents being housed synchronously within a single organism is one that has not been met with theoretical and empirical favour, as it is usually associated with incoherent behaviour on behalf of the organism. However, as the octopus departs significantly from the vertebrate models that are presupposed by discussions on cognitive agency, there are principled reasons to believe that received views on cognitive agency may not be applicable to it at all.

The flow of Part II is as follows. Chapter 3 demonstrates the extent to which octopus cognition—especially with regards to motor control—comes in an embodied, dynamical format. Chapter 4 argues that, while the dynamical components of octopus cognition cannot be accounted for representationally, other cognitive routines call for a representational framework. Together, Chapters 3 and 4 establish the ontological heterogeneity of octopus



cognition. Finally, Chapter 5 explores how the octopus raises questions pertaining to whether cognition presupposes a cognitive agent, and the number of cognitive agents that can be present within a single organism. The subject matter of Chapter 5 enables a smooth transition into Part III, which discusses similar issues from the perspective of an investigation into consciousness.

## PUTTING AN ARM ON IT:

### EMBODIMENT IN OCTOPUS COGNITION

The present chapter demonstrates that, in the octopus, motor control—a significant component of cognition—is largely *embodied*, or substantively inextricable from the physical condition of the body in action. In order to do this, it will be argued that three major defining features of embodied cognition are instantiated in the octopus. These features are 1) decentralization of the cognitive system, 2) processing and control operations that are intrinsically non-representational, and 3) generation of vital information about the body through the *dynamical* or causally interdependent behaviour of the arm muscles. The discussion then turns to examining how embodied motor control routines stand in relation to the rest of octopus cognition.

#### 3.1 Introduction: Traditional approaches to cognition

For the greater part of the history of cognitive science, *computationalism* has been the dominant framework used to understand the mind and its workings. Due to its long and established history, the computational framework can be referred to as the *traditional* view. As is inevitable within any paradigm, there is variation within computationalism; nevertheless, it is possible to provide an overview of its main ideas. Computationalism equates cognition with *computation*, in the sense of processes comprised of distinctly identifiable steps used to manipulate information-bearing states or entities, which are known as *representations*. Consequently, cognitive systems have long been construed as computers, in the sense that they carry out computational processes by which information is extracted from input states and used to produce behavioural output. Input states—the

basic form of which is sensory information—are then converted or *transduced* into a format accessible to the system’s processing mechanisms.

The computational format employs representations, which are mechanisms that respectively stand in for, or represent, the information contained in input states; early strands of computationalism specify representations as being *symbols*, an idea that held sway for a long period of time. Representations are subjected to computational processing by which the information they bear is used to generate output commands that are transmitted to the effectors, thereby generating behaviour. They can also be recombined, giving rise to sophisticated representational states that bear complex information. In order to ensure the coherence of these compounded representations, the combinations any particular representation can enter into are inherently restricted by the operations that process it. Likewise, specifications as to how representations are to be combined and the sequence of operations by which they are to be manipulated are encoded into the causal structure of the operations processing them (Fodor 1975).

As a consequence of its theoretical stance, computationalism entails certain commitments to the functional organization of cognitive systems and to the contributions of the physical entities that instantiate them. Within the context of biological cognition—which is what this thesis is concerned with—such commitments pertain to the respective roles played by the brain and the body. The notion of representational symbols arose as a solution to the problem of integrating input that comes in dissimilar modalities (Newell and Simon 1961). The sensory systems are the body’s primary sources of information about the world (and its internal states), and their input is vital to how the organism navigates within it. However, the different sensory systems respond to distinct types of stimuli, and consequently the information with which they provide the organism is modality-specific. In order to be put to use efficiently and effectively, these sensory states must be consolidated—but how is consolidation possible given their heterogeneity? The solution came in the form of transducing raw sensory input into modality-neutral symbols that retain the information provided by sensory states, but without the modality-specific features that prevent it from being globally accessible within the cognitive system.

Transduction and consolidation of input into modality-neutral, globally accessible symbols can be carried out only by a mechanism that has access to all the subsystems constituting the cognitive system and that can handle as many modalities as the cognitive system supports—in other words, a central mechanism that functions as both processor and controller. Computationalism therefore entails a commitment to the notion that only

functionally centralized physical systems can implement and subserve cognition. With respect to biological organisms, such a commitment identifies the brain as the central cognitive mechanism, and gives rise to a corollary that specifies having a centralized nervous system as a necessary condition for an organism to be capable of supporting full-fledged cognition.

Under the traditional view, cognition begins with transduction; and since transduction operations are carried out in the brain in biological systems, the brain is equated with the cognitive system (van Gelder 1995). While the body functions as the organism's interface with the world, it is not an indispensable component of the cognitive system: the contribution of the body goes only as far as supplying the brain with sensory input. Once this input has been transduced, the "body and the physical environment [can be] dropped from consideration" (van Gelder 1995, 373). As such, if the brain were to be supplied with input that mimics or is functionally equivalent to that provided by the body, cognition would proceed unhindered (Shapiro 2011). The traditional view thus takes a disembodied stance toward the nature of cognition, in that it maintains that cognitive processing is not necessarily dependent on the actual flesh-and-blood structures realizing it.

The dominance of the computationalist paradigm is no accident: its main explanatory tool, representations, has had unparalleled success in accounting for intelligent behaviour. Representations make it possible for a wide range of information to be stored, enabling it to be retained, accessed and utilized even in the absence of the relevant stimuli, i.e., when the cognitive system is *offline*. The stimulus-independence afforded by the ability to function offline entails that the cognitive system is not limited to utilizing information about occurrent sensory states. Because a representation-using system can carry on its operations without the need for a constant stream of sensory input, the range of informational states available to it is broadened considerably.

Offline cognition entails that the information contained in representations can be retrieved without the need for sensory triggers. The minimal physical constraint on the accessibility of representations allows them to be manipulated in more ways and thus generate more content than would have been possible had they been dependent on occurrent stimuli. Such manipulations include counterfactual or hypothetical constructions, novel combinations, and accessing past- or future-oriented information. These operations expand the system's information storage and processing capacities, consequently setting the stage for sophisticated cognitive abilities such as planning, decision making, problem solving,

mental time travel, and a theory of mind, all of which are considered hallmarks of advanced intelligence. It thus comes as little surprise that representation use has long been held as the distinguishing feature of cognition, and in biological organisms, minds (Sterelny 1995; Adams and Aizawa 2010).

Although they have been highly successful, representations are not without their share of problems. For instance, a major challenge faced by the traditional view—and one of the main reasons cognitive science has started to look to other accounts that are less dismissive of the role of the body—is known in the literature as the *symbol grounding problem*. The disembodied nature of representational symbols raises the question of how they acquire meaning. For instance, how does any mental representation for redness represent and stand in for the colour red? One flaw that the traditional view has is that it takes transduction for granted; a causal account of how input—especially of the sensory type—is transformed into symbols is conspicuously lacking. Without such an account to close the explanatory gap, representations appear to map onto their respective content *arbitrarily*—something that the traditional view has long been satisfied to accept without much question. In traditionalists' books, it is not necessary for representations to bear any inherent isomorphism to the content they stand in for, so long as they are consistent in doing so.

Thus, the characterization of cognition yielded by the traditional view (especially in its early forms) is as such: cognition is the algorithmic manipulation of representational symbols that are arbitrarily assigned to their respective content. However, such a construal does not fully capture the nature of biological (or at least human) cognition. While cognitive processing can be described in terms of rule-based symbol manipulation, it can be done so only to a certain extent. As has been demonstrated by John Searle (1980) in his famous Chinese Room thought experiment, this thoroughgoing computationalist account leaves out understanding, a qualitative feature which is intuitively accepted to be a vital component of cognition. The indispensability of a qualitative aspect of cognition is further illustrated by Frank Jackson (1982; 1986) when he argues that Mary, a brilliant scientist who has never seen any colours but black and white and grey, yet knows all the quantifiable physical properties of red, experiences something new when she sees a red object for the first time. Theoretical concerns such as these have prompted philosophers of mind to question the traditional view and investigate whether the body is a more active contributor to cognition.

This is where the *embodied cognition* movement comes in to buck tradition. Again, there are many streams within embodied cognition, each challenging the traditional view

from a different angle. However, they are all variations on the theme that cognition is inextricable from the physical components and features of the agent's body. Depending on how this claim is interpreted, the relationship between the traditional and embodied views ranges from opposition, to compatibility, to complementarity (Shapiro 2011). One of the major battles within the debate is fought over representations. Some moderate positions in embodied cognition (e.g., Barsalou 1999) adopt the notion of representations but reject the view that they are of a symbolic nature, whereas radical ones (e.g. Chemero 2011) reject representations altogether.

Another bone of contention between traditional and embodied views pertains to the nature of cognition. Traditionalists hold that the structure of cognitive processing is computational or algorithmic, involving a fixed sequence of operations by which input is used to produce output. In contrast, embodied accounts are better at capturing the fluidity of cognition and the participation of the body and the environment in cognitive processing. Embodied approaches to cognition have been highly successful, although there are aspects of cognition that they still handle less well than their traditional counterparts. However, these explanatory shortcomings are mainly because of embodiment's youth and immaturity. Importantly, embodiment has the powerful advantage of having empirical data on its side. (This will be discussed in more detail as the thesis progresses.) This accrual of explanatory and empirical success poses a strong challenge to the traditional view, as it provides ever-growing evidence that cognition might not be wholly computational, or even not computational *at all*.

This is where the octopus comes in. The cognitive architecture of the octopus is a clear deviation from the traditional model of cognition, i.e., a centralized control system whose output is the result of algorithmic processing of representations. Instead, the octopus nervous system is characterized by functionally autonomous components, decentralized motor control and sensory processing, non-computational muscular operations that are vital to goal-directed behaviour, and minimal central proprioceptive monitoring of the body. In addition to being radically different from traditional cognitive models, these features of the octopus nervous system stand as organic parallels to a number of salient functional principles endorsed by embodied cognition. In particular, the octopus instantiates three of the major ways in which a cognitive system is characterized as embodied: having a decentralized control architecture (Brooks 1991), non-representational operations (van Gelder 1995), and *dynamical* processing (Thelen et al. 2001).

### 3.2 Traditionalism vs. Embodiment

How exactly do traditional and embodied views stand in relation to each other? The discussion in this section explores whether they are incompatible or reconcilable. The lynchpins of the debate are how representations and computation—the standard bearers of traditional cognitive science—are received and regarded. Supporters of embodiment may reject one or both to give rise to radical opposition to traditionalism; or one or both can be reimagined and adopted into the fold of embodiment, resulting in compatibilist views. This section presents an overview of the general positions within the traditionalism-embodiment debate.

The radical *anti-representationalist* camp rejects representations outright, on both ontological and epistemic grounds (Chemero 2011). Its ontological claim is that representations are not actual entities, but are merely theoretical constructs used to explain cognition. Its epistemological stance is that talk of representations should be avoided or eliminated in accounting for cognition. Thus, ontological anti-representationalism unequivocally dismisses the *existence* of representations, while epistemic anti-representationalism challenges the *use* of representations in theories of cognition.

Moderate approaches may accept the notion of representations, but reject the symbolic, disembodied, and arbitrary nature attributed to them by traditionalism. Instead, these representationalist embodied accounts hold that input from the sensory systems of the body is crucial to fixing the content of representations. Thus, what can be referred to as *embodied representations* retain their modality-specific properties. Adopting this embodied stance sidesteps the closely related problems of how input is transduced and how representations acquire meaning, the major challenges besetting traditionalism. (As the subject of representations is a hefty one in itself, it merits a separate discussion of its own; one will be provided in the next chapter.)

Another moderate position allows that cognition may have computational components, but does not confine their substrates to the brain (Wilson 2004; Shapiro 2012). Instead, the body and even the environment are regarded as indispensable contributors to cognition. While the bulk of cognitive processes take place in the brain, some of the information-bearing states they operate over are physically realized outside of it. The activity of the sensory systems of the body generates states that already contain information that can be used locally or accessed by cognitive mechanisms found in the brain. Because raw sensory input is already information-bearing, there is no need for it to be transduced

into representational symbols. The movement of the body is another source of information that is vital to cognition (Noe 2004; Gibson 1979). Whenever the organism shifts its position, the angles from which its sensory receptors are stimulated change. The state of flux that is the activity of the sensory systems results in the organism's information about the world being updated in real time. This embodied sensorimotor information can then be recruited by brain-based cognitive mechanisms that carry out computational processes over it. This way, cognitive processing retains its computational nature, but is infused with embodied elements.

If embodiment is to succeed in its attempt to claim the paradigmatic throne, it needs to provide a plausible explanatory toolkit to replace the one it supplants. Hence, *dynamical systems theory* has been fielded as the explanatory framework by which cognitive processes are described from an embodied perspective (Chemero 2011). Dynamical systems theory is the mathematical apparatus used to quantify and predict the behaviour of *dynamical systems*, or systems in which the individual behaviour of each component has reciprocal or *coupled* causal influence on that of the others.

Construing cognition as being of a computational nature has been criticized as rendering it as static and inflexible, unable to capture the temporality of the causal contributions of the body and the environment to cognitive routines. Instead, the fluidity of the interactions between the brain, body, and world are more accurately understood as dynamical systems; such is the position endorsed by another major thread of embodiment, *dynamicism* (van Gelder 1995). While dynamicism can be subdivided into representationalist and anti-representationalist streams, the main attack it launches on traditionalism centres on the format of cognitive processing: it rejects the idea that cognitive processes consist of discrete steps executed according to a fixed order. Rather, cognition is better construed as the *state evolution* of a cognitive system, or the summation of the continuous changes it undergoes over time as the result of the coupled interactions of its components.

That the various sensory systems of the body uniquely respond to different types of stimuli is an important feature of embodiment. That their activity yields information-bearing states that can be directly and immediately utilized by cognitive mechanisms, or what Andy Clark (2008) refers to as *self-structured information*, is another. In other words, sensory input is information-bearing from the source. Due to its embodied nature, the sources of sensory information are *non-redundant*, in that sensory information of any modality can be generated only by its system of origin.



This leads to another vital feature of embodiment: the distribution of the cognitive workload between the brain and the body, i.e., between neural and non-neural corporeal mechanisms. Thus, the sensory systems of the body—not just the information they generate—can be considered constituents of cognition (Shapiro 2011), or even of cognitive mechanisms. As such, the production and processing of sensorimotor elements of cognition are mostly the responsibility of the body, and not the brain as traditionalism would hold. Such a division of labour is referred to by Clark (2008) as *nontrivial causal spread*, as the contributions of each component of the cognitive system are unique and irreplaceable. The dependence of sensorimotor information on the physical structure of its source systems further entails that the kind of body an organism has shapes or influences how its cognition is realized (Varela et al. 1992).

### **3.3 Decentralization**

The octopus has been identified as an excellent case study in embodied cognition (Hochner 2012). Due to the functional organization of its nervous system, it instantiates a number of features claimed by embodied cognition as its trademarks. To begin with, the octopus nervous system exhibits considerable functional decentralization; peripheral sensorimotor processing and control routines do not require central involvement. Although decentralization does not guarantee that a cognitive system is embodied, it entails that processing operations are distributed between the system's components. Likewise, while concluding that distributed processes are embodied may not be the necessary next step from accepting that they are carried out locally, it is nevertheless a natural one. In other words, functional decentralization and distribution are organizational features conducive to embodiment.

An early breakthrough in the embodied cognition movement was the construction of intelligent, adaptive robots that made use of a decentralized control organization. Developed by Rodney Brooks (1991) and his lab, these robots, or “Creatures,” as they were called, were tasked with going about their business in the real world; in particular, they had to move around in an office environment without bumping into things. While this task seems to be trifling, it is more challenging than it first appears. Like any other natural environment, an office is full of stationary and moving obstacles to the Creature's path. Thus, it would have to integrate sensory input with motor output in order to keep track of

the changes in its surroundings and adjust its trajectory in real time, thereby exhibiting a rudimentary form of adaptive behaviour.

What is significant about the Creature is that its control architecture is decentralized and non-representational. Known as the *subsumption architecture*, it is comprised of hierarchically organized autonomous subsystems that “decide when to act for themselves” (Brooks 1991, 146). Every subsystem, or *activity layer*, is dedicated to a specific function, which determines how it processes input and produces output. That is to say, due to the functional dissimilarities between them, the layers may receive the same input, but extract different aspects of information from it and generate different types of behaviour. Thus, processing and control is not the responsibility of a single, centralized mechanism, and the Creature’s overall behaviour is a conjunction of the distinct contributions of autonomous subsystems. The complexity of a Creature’s behaviour depends on how many layers it has, as the subsumption architecture’s design principles allow it to accommodate multiple, incremental layers. This way, output from lower layers can update the information of higher ones, ensuring that the motor commands generated by the latter remain appropriate.

To illustrate, Brooks explains that a first-level motor control layer might be responsible for avoiding obstacles, and would thus use information from the Creature’s sensors to register the positions of the various objects within its sensory field. Meanwhile, a second-level layer in charge of navigation would employ the very same sensory systems, but would use the input to plot the path along which the Creature is to move. Thus, the first-level layer is in charge of moving the Creature *away* from an obstacle, while the second-level layer directs it to move *toward* something. To ensure coherence in overall behaviour, the second layer must have access to the output of the first, which it incorporates into its navigational commands. However, neither layer participates in the actual operations of the other, so that they remain functionally autonomous, and *operate in parallel*.

Brooks points out that the control organization of the subsumption architecture eliminates the need for central representation, as processing responsibilities are distributed among the various layers. Nevertheless, he admits that there are critical issues about the behavioural complexity permitted by a decentralized control architecture that must be addressed. Due to its hierarchical organization, the extent to which layers can be added without the system collapsing is an important consideration. In centralized systems, the central mechanism integrates and synthesizes the dissimilar input of multiple contributors, and is solely responsible for generating motor output; thus, the degree of behavioural complexity of a centralized system depends mainly on the capacities of this mechanism.

On the other hand, the subsumption architecture's lack of a processing and control locus calls into question the extent to which the different layers can access each other's information to produce multifaceted and coherent behaviour. These same constraints also raise doubts about whether an artificial system constructed according to the subsumption architecture can support complex, high-level functions.

Whether a decentralized cognitive system is also embodied depends on whether its contributing subsystems self-structure their respective input into information-bearing states that can already be utilized in their basic form, and further recruited into complex operations. What makes the subsumption architecture an exemplar of an embodied system is not its decentralization *per se*, but that its constituent layers self-structure information. Speaking of modalities may be misleading, but a non-organic parallel can be drawn between the layers of the subsumption architecture and the sensorimotor systems of a biological organism: each layer would have been constructed and programmed in a unique way that would allow it to extract specific information from the input it receives and use it in a manner idiosyncratic to its designated function. Likewise, the octopus arm nervous system, with the autonomy of its sensorimotor routines, counts as a network that self-structures information, and thus fits the embodiment bill. Furthermore, due to the extent of its processing and integrative operations, the axial nerve cord has been proposed to be an “alternative control center for high-level information processing” (Richter et al. 2015, 1069).

The discovery that octopus arms have extensive sensorimotor processing responsibilities was an early one, with Rowell's (1963) experiments on amputated arms being among the first to demonstrate such findings. One of these was that tactile stimulation to the suckers elicited grasping—and could do so for up to three hours after amputation. These results indicated that control of the grasping reflex is contained within the suckers and sucker ganglia. The same study also reported that pricking a freshly amputated arm with a pin resulted in flinching of the skin around the area, the arm moving away from the direction of the stimulus, and the arm and suckers orienting themselves toward the stimulus—all identical to the responses exhibited by an intact octopus.

More recent studies on arms that had been neurally disconnected from the brain provided more insights on the extent of peripheral motor control. Consistent with Rowell's findings, stimulating the muscles or the ganglionic sections of the axial nerve cord causes the muscles to contract, indicating that reflex control is a peripheral responsibility. It was

also discovered that electrical stimulation to the axial nerve cord in parts where it contains axon fibres from the brain evokes waving movements or partial arm extensions (Sumbre et al. 2001). However, because the commands that initiate extension are centrally issued, as are those also pertaining to orientation, direction, and velocity, a full arm extension can be generated only with the participation of the brain (Sumbre et al. 2001). These findings are of the utmost significance, as they demonstrate how motor control responsibilities are distributed between the brain and the arm nervous system, particularly with regard to where the various constituent sub-routines are localized. Thus, “there appears to be an underlying motor program embedded in the neuromuscular system of the arm, which does not require continuous central control” (Sumbre et al. 2001, 1847).

The schema of motor control in an octopus can be summarized as such: the brain issues high-level global motor commands, while the arm nervous system supplies the kinematic parameters that specify the spatiotemporal details of movement. Thus, it can be said that central motor commands are quite literally fleshed out within the periphery. This division of labour has been heralded as a unique biological solution to the challenge of motor control posed by a flexible body with no internal proprioceptive landmarks (Sumbre et al. 2005).

The extensiveness of sensorimotor operations within the arm nervous system significantly diminishes the workload that would otherwise have been delegated to the brain. It can be said that these processing and control responsibilities have been off-loaded into the periphery, thus exhibiting a defining characteristic of a decentralized cognitive architecture. As each arm processes the input it receives and uses it as needed in local routines, there is no need to transmit it to the brain in its full detail. Furthermore, as a consequence of its lack of somatotopic representation, the brain is unable to localize sensorimotor information originating from the arms with respect to the octopus’s body (Zullo et al. 2009). While the direction of causation depends on which between the absence of somatotopy and delegation of sensorimotor routines to the periphery was the prior evolutionary development, it is accepted that these two features of octopus cognition co-evolved due to one another. In other words, extensive peripheral processing and control is correlated with the absence of a need for central somatotopic representation (Zullo et al. 2009). It is believed that what is represented in the brain is information about active motor programs, which are likewise encoded using neural circuits that are not somatotopically organized (Zullo et al. 2009). Again, the brain would receive information that the octopus

is moving in a particular way, without being able interoceptively to pinpoint the arm or arms concerned.

Significantly, peripheral sensorimotor routines are not responsible just for low-level or reflex actions but are also indispensable components of goal-directed behaviour. Goal-directed behaviour is controlled centrally, not just because the brain is the main control centre, but also because it requires consolidated information from various cognitive domains and sensorimotor systems. Two such systems that are of the utmost importance to motor control in general are *proprioception* and *kinaesthesia*, which provide information about the position and movement, respectively, of the body and its parts. Furthermore, the skeleton and joints are extremely important when it comes to structuring this spatial information. They limit the degrees of freedom of movement that are available to the organism, and serve as fixed or semi-fixed points against which the body's posture and motion can be relativized. Thus, in skeletal animals such as vertebrates, the inherent physical constraints imposed by the bones and joints help to shape the spatial aspects of motor commands. In contrast, the octopus's lack of a rigid skeleton entails the absence of interoceptive points of spatial reference, and so the information generated by its proprioceptive and kinaesthetic mechanisms is not as fine-grained and well-structured as that of vertebrates. Furthermore, the higher motor centres of the octopus brain do not receive detailed proprioceptive input about the physical condition of the arms. Consequently, the global motor commands issued by the brain do not—and cannot—specify the spatial details of how the movement is to be actualized, as they do not have the neural equipment to allow them to exert control over particular portions of the arm. Instead, these spatial parameters are supplied locally by the arm nervous system.

As an evolved means of overcoming the challenge of motor control in such a flexible organism, the octopus makes use of stereotypic motor patterns that are incorporated into its various types of natural behaviour (Sumbre et al. 2001; Gutfreund et al. 1996). These stereotypic motor patterns simplify motor control by narrowing down the degrees of freedom of its arms to a manageable number, to control movement along the vertical, horizontal, and longitudinal axes (Gutfreund et al. 1996). Interestingly, the details of these motor patterns are not encoded in the brain, but remain entirely within the arm nervous system (Sumbre et al. 2001).

While stereotypic movements are innate and display little sensitivity to learning, octopuses have been found to be capable of modifying or deviating from them when met with physical constraints or tasks that require departure from these fixed motor patterns

(Richter et al. 2015; Gutnick et al. 2011). It is believed that control of these modifications involves the use of sensorimotor feedback from the muscles, skin, and suckers. This feedback would be incorporated in real time into peripheral-level motor commands, and is likely to be responsible for continuously ensuring the correctness of the arm's trajectory as it executes a movement (Gutfreund et al. 1998; Gutfreund et al. 2006). Again, due to the neuroanatomical features of the octopus, this information remains within the periphery and does not reach the brain, further underscoring the autonomy of the arm nervous system when it comes to self-structuring information.

One such stereotypic movement is *bend propagation* (Gutfreund et al. 1996), which is used to extend the arm. It involves forming a bend at any point in the arm, and stiffening the musculature so that the bend is pushed distally toward the arm tip. Another is *pseudo-joint articulation* (Richter et al. 2015), which is of greater cognitive interest, as it is an example of how dynamical muscle activity is used to fix the location of a temporary anatomical structural arrangement whose precise placement is crucial to the success of the movement. Used in *fetching*, or bringing objects to the mouth, pseudo-joint articulation is characterized by forming bends in the arm that are functionally analogous to the joints of the human arm; as a result, the motor profile of fetching in an octopus matches that of the human arm when the hand reaches for the mouth (Sumbre et al. 2006).

In pseudo-joint articulation, the octopus forms what is referred to as the *medial bend*, which corresponds to the human elbow, and uses it as a pivot point around which the distal segment rotates; the *distal bend*, which corresponds to the wrist, marks off the segment closest to the arm tip, with which the retrieved object is grasped. The location of the medial bend determines the accuracy of the movement: if it is too high the arm will overshoot, and if it is too low then the arm comes short of the mouth. At this point, a puzzle arises. If goal-directed behaviour is centrally controlled, yet the brain does not have the benefit of mechanisms that simplify motor control, i.e., somatotopic mapping, proprioception, and skeletal articulation, how is the octopus able to pinpoint the exact location where the medial bend must be formed? The answer lies in another paradigmatic realization of embodiment: non-representational operations of a dynamical nature.

### 3.4 Non-representational operations

The notion that the physical state evolution of a system—i.e., the interdependent spatiotemporal changes undergone by its components—could be informational was best

captured by Tim van Gelder (1995), when he asks whether cognition can be anything other than computation. Answering positively, van Gelder sets out to do two things: to demonstrate that a thoroughly non-representational account can successfully account for adaptive behaviour and to endorse the dynamical approach to cognition as a viable alternative to computationalism. This section will focus on the non-representational aspect of dynamicism.

To make the case that cognition can be construed not just computationally but also dynamically and non-representationally, van Gelder presents James Watt's centrifugal governor (or, simply, the *Watt governor*) as an exemplar of a non-representational system whose arguably adaptive behaviour is the outcome of its dynamical state evolution and not computational algorithms. As van Gelder regards representations as the cornerstone of computationalism, rejection of the former entails rejection of the latter. He presents a particular task, and compares how the Watt governor carries it out through the use of dynamical operations with how its hypothetical computational counterpart would do it. This demonstrates that dynamical and computational systems can both be successful at performing the same task, but in thoroughly dissimilar ways.

An Industrial Revolution breakthrough, the Watt governor was developed to address the need to provide steam-powered engines with a steady, reliable, and even flow of steam. Such engines usually used a flywheel whose rotation speed was affected both by the pressure emitted by the steam boilers and by the engine's workload, consequently producing an irregular supply of steam. To regulate the speed of the flywheel, a throttle valve had to be continually adjusted to compensate for the inconstancy in steam supply. This could be done manually by a technician—or more efficiently by a device called a governor.

The Watt governor, whose design principles were based on windmill technology, consisted of a spindle with two hinged and weighted arms. It was attached to the flywheel in such a way that the speed of its rotation was directly dependent on that of the flywheel. The centrifugal force generated from the speed of the flywheel caused the spindle's rotation to slow down or speed up, in the process respectively lowering or raising its arms. Lowering the arms caused the valve to open and let more steam through, while raising them closed the valve and obstructed the steam's flow. The result of such compensatory movements was an even and steady flow of steam.

Van Gelder contrasts how the Watt governor works with the way a hypothetical computational governor would. Unlike the Watt governor, the computational governor is

representation-dependent and operates algorithmically. The algorithm involves the following discrete and ordered steps: measuring the current speed of the flywheel, comparing it against the required speed, remediating discrepancies between the actual and the required speed by calculating compensatory steam pressure, and making the necessary adjustments to the throttle valve based on the results of this calculation. All these states involve representations to stand for the states of the different operational components of the governor, whose output is generated through the use of rule-based operations by which these representations are processed. The steps of the algorithm take place according to a fixed sequence, which is repeated as many times as are necessary to stabilize the steam flow.

According to van Gelder, there are four properties inherent to computational systems, all of which are absent from the Watt governor: “representation, computation, sequential and cyclical operation, and homuncularity” (van Gelder 1995, 351), with the last item referring to the division of processing labour between specialized subsystems that then communicate with each other to consolidate the information they generate. Van Gelder argues that the lack of these properties is a consequence of the fact that the Watt governor is thoroughly non-representational; on his account, there is simply nothing in it that could support, much less generate representations. The physical states of the Watt governor do not stand in for information of any sort. Rather, it is the fluid transition of the governor’s individual components from one set of spatial coordinates to another over time, i.e., its state evolution, which produces its behaviour. Consequently, because there are no representations, there can be no computational algorithms either, as they have nothing to operate over.

Instead, the overall behaviour of the Watt governor arises as a result of the *coupled* or causally interdependent interactions of its components, whereby each individual element’s behaviour affects and is affected by that of the others. Thus, the state evolution of the Watt governor is brought about by the continuous physical changes undergone by its components, and not computational processes constituted by discrete steps that follow a fixed order. This real-time state of flux thus stands in sharp contrast to the third characteristic of computational systems identified by van Gelder, sequential and cyclical operation. Consequently, the behaviour of the Watt governor—and dynamical systems in general—is best expressed through the use of differential equations, rather than computational algorithms.



Finally, coupling also dislodges the need for homuncular information transfer. Computational systems often decompose into specialized modules dedicated to various subtasks, e.g., one module to process colour, another to process shape, and so on. The output from these modules is then consolidated, normally by a central processor and into the form of a compound representation, and made available to the effector systems. By contrast, the coupled interactions between the components of a dynamical system entail that while they each perform their respective functions, they all have direct influence on each other's output. As each element behaves within the system in a unique way, its individual state evolution generates a different facet of information, which is consolidated in real time with that arising from the others to which it is coupled. Thus, the state evolution of the whole system is the outcome of the coupled interactions of its components, whose causal fluidity is reflected in the structure of the overall information-bearing state it generates.

In the previous section, the question was raised as to how the octopus is able to determine the exact point on its arm at which the medial bend is to be formed, without the benefit of somatotopy and proprioception. The proffered answer was that non-representational dynamical operations are what make this motor control task possible. In his account of the Watt governor, van Gelder demonstrates how mechanical operations that involve the dynamical interactions of physical structures can give rise to information-bearing states. While this information may remain within the level at which it is generated—i.e., it is used only by the very system whose operations produce it—it may also be recruited into more complex control and processing routines.

Octopus fetching movements are a notable example of such a cognitive routine with a significant dynamical component. The general profile of a fetching movement is provided by centrally issued motor commands, but the crucial task of pinpointing where the medial bend is to be formed is executed through the dynamical muscular activity of the arms. It is of the utmost importance to note that determining the location of the medial bend takes place without the participation of the brain. When the arm grasps an object, waves of muscle activation are triggered at the point of contact. Due to the hydrostatic organization of the arm musculature, these waves ripple throughout the length of the arm in both directions between the base and the tip. The point where these waves collide is where the medial bend is formed (Sumbre et al. 2005; Sumbre et al. 2006; Richter et al. 2015). Thus, determining the precise location of the medial bend is a task performed entirely within the periphery, through the state evolution of the arm musculature.

What this distribution of labour demonstrates is that substantive aspects of motor control—a major cognitive domain—can be offloaded to the effectors themselves. More importantly, these subroutines can be executed through non-algorithmic, dynamical mechanical processes that do not support representations. The distinct contributions of the brain and the arm to the control of a fetching movement are non-redundant and idiosyncratic. In other words, the types and formats of information-bearing states they respectively give rise to are inextricably dependent on their physical substrates. Consequently, information generated by brain-based operations cannot be sourced elsewhere in the octopus nervous system, and likewise for arm-based information. Thus, the control routine for fetching decomposes into 1) central commands to activate the movement, specify the velocity at which it is to be executed, and set the general trajectory along which the arm is to travel, and 2) peripheral operations that fix the spatial parameters of the arm. Furthermore, the absence of central somatotopic representation and proprioception ensures that positioning the medial bend cannot be carried out by brain-based cognitive processes.

### **3.5 Dynamical processing**

After establishing that cognition *can* be dynamical and not just computational (van Gelder 1995), the next move is to demonstrate *how* to account for cognition dynamically. An influential study led by Esther Thelen (Thelen et al. 2001) undertakes this very task in its treatment of the *A-not-B error*, a perceptuo-motor phenomenon peculiar to infants within a certain age range. In this landmark paper, Thelen and her team provide an alternative to traditional models of cognition: their approach presents cognitive processing as the dynamic interplay of psychological, developmental, and environmental factors, and does not use representations in its explanatory framework.

First described by Jean Piaget, the A-not-B error is an example of perseverative behaviour exhibited by infants from seven to twelve months old. Experiments to elicit it involve hiding a toy under location A within full view of the infant, who is then allowed to reach over to retrieve it. The process is repeated several times in succession. The toy is then transferred to location B, again with the infant watching. After a delay of a few seconds, the infant is allowed to retrieve the toy. However, instead of reaching over to B, the infants would reach toward A, even though they had seen the toy being hidden under B.

A number of explanations for the A-not-B error have been offered, such as discrepancies between the infant's visual input and motor output, insufficiently potent object representations, underdeveloped motor control, poor memory, and inability to inhibit motor responses. In various ways between them, these explanations presuppose that cognition is representational, and identify the main culprits as inchoate representations and dissonances between perception and motor control. In contrast, Thelen et al. (2001) do away with talk of representations altogether. Instead, they attribute responsibility for the A-not-B error to the inextricably interdependent interactions of age-specific perceptual, motor, and memory processes. As these processes all have neural correlates, neural activity, rather than representations, can be identified as the fundamental vehicles of cognitive processing. Neural activity, somatic activity, and environmental factors relevant to perception and movement, and their coupled interactions with each other all take place within a *dynamic field*, or the set of spatiotemporal coordinates in which the state evolution of a dynamical system is realized. Importantly, all these elements can be quantified through the use of differential equations. Thus, Thelen et al.'s dynamical model of cognition is a physicalist one that does not make use of spooky notions such as representations.

Thelen et al.'s account holds that the A-not-B error arises out of "a motor planning process that is part of a dynamic perception-action loop" (Thelen et al. 2001, 11), rather than being the outcome of discretely identifiable and causally distinct cognitive routines. A number of physiological factors were identified as contributing to perseveration. To begin with, how well-developed the visual system and visual processing mechanisms are determines the extent to which they can disambiguate and structure the input they receive to generate information to be used in motor control. Over the course of the experiments, it was discovered that reinforcing the stimuli so that they provided stronger visual cues and held the infants' attention for longer diminished perseverative behaviour. Unsurprisingly, memory also plays an important role; as the capacity for retention increases, infants are better able to remember that the object is at B. Furthermore, repeating an action reinforces motor memory of it, hence perseveration can be partially explained by the infant's being physically habituated to reach toward A several times before shifting over to B. Finally, because perception and motor control are closely intertwined, the refinement of perceptuo-motor planning and decision making such as that involved in the reaching task depends on how well-developed the individual constituent operations are, as well as the extent to which they are integrated with each other.

The dynamical account of motor control is detailed as follows. Neural evidence strongly suggests that action planning and the formulation of motor commands take place simultaneously. Populations of neurons have been discovered to fire collectively to generate *vector codes*, or commands that specify motor trajectories. These codes reflect a body-centred orientation, such that the motor trajectory they prescribe remains directed toward the target regardless of the subject's position. Importantly, the vector code is not complete and unmodifiable when it is first generated, but is updated in real time during the interval between initial perception of the target and the actual reach toward it, and as the subject moves. Thus, updating the vector code not only involves motor feedback but visual input as well. This way, the vector code is gradually and continuously adjusted and refined as the action unfolds. It has also been discovered that when an action is delayed or not executed immediately, neural activity nevertheless reflects the intended motor trajectory, indicating that the vector code also predicts how the movement is to unfold. Memory enables the relevant systems to retain several aspects of information about an action, such as the position of the target it is directed toward, the spatiotemporal parameters of the movement, and how the actual execution of the movement feels. With every instantiation of that action, the memory of it is reinforced, so that it tends to “bias subsequent movements” (Thelen et al. 2001, 14).

In summary, the dynamic field within which motor control takes place is one where input from various systems or domains that contribute to cognition are integrated. As the dynamic field evolves, it continuously generates and sustains neural activity that codes for motor trajectories, and adjusts them in real time as it incorporates the sensorimotor feedback that arises as an action is being executed. The capacity for planning and predicting future movements—an important aspect of motor control—is made possible by the memory component of the dynamic field. Thelen et al.'s model captures not just the fluidity of cognitive processing but also how it is constrained by temporal factors such as the infant's current developmental stage. Thus, it recognizes an important feature of biological cognition, which is that the developmental timeframe of an organism influences the degree of maturity of its cognitive mechanisms and capacities.

In contrast, computational frameworks take a much more linear and representation-dependent approach. To begin with, they construe motor control as the process of selecting the degrees of freedom of movement to bring the relevant effectors into the spatial coordinates or geometric shape appropriate for the intended action (Wolpert 1997). The range of degrees of freedom available to an effector depends on its anatomical structure,

with greater flexibility affording more opportunities for movement. Furthermore, most motor tasks can be completed using different types of actions, each of which entails its own set of degrees of freedom for the way the effectors are to be used. Thus, motor control is the process of identifying which motor patterns to activate, by specifying the degrees of freedom required to execute them. Once the degrees of freedom have been selected, the next step is to generate the commands to actualize them. This involves transforming the intended spatial coordinates of the effectors into actual muscle activity, in what is known as the *inverse problem*. The process of resolving the inverse problem is detailed as following a hierarchical sequence of subroutines by which motor commands become more specific along the way (Wolpert 1997). It begins with neural commands, from which those pertaining to activating the muscles are received by the motor system. These activation commands then undergo further filtering by the motor system to extract information regarding the overall geometric shape the effector is to take. Additional refinement of the motor command specifies the path the effector is to travel along in order to execute the movement, with reference to external or target markers.

While more than one hypothesis has been put forward as a solution to the inverse problem, what they have in common is that they make use of internal models that specify both the position of the limbs, as well as which limbs can be manipulated in order to incorporate changes brought about by their movement. The information generated by these models is then used to formulate the commands to activate the muscles appropriately. Likewise, the possibility of anticipatory motor control functions is attributed to the use of a *forward model*, which “[captures] the forward or causal relationship between inputs to the [motor] system...and the outputs” (Wolpert 1997, 212). That is to say, forward models provide information about the current sensorimotor state the organism is in, on the basis of which it anticipates future states that it is likely to occupy. A number of important functions have been attributed to forward models on account of their predictive properties. Among these are helping the motor system to distinguish between *reafferent* (or self-generated) and *exafferent* (or externally generated) movements and sensations, keeping the motor system stable in the event of feedback delays, predicting the effects of actions, and consolidating sensorimotor information (Wolpert 1997). Computational models do not differ from dynamical ones in acknowledging the integration of sensory—especially visual—input, proprioceptive information, and memory as essential to motor control. However, computational accounts presuppose that “these processes involve internal

representations of the target and limb positions and coordinate transformations between different internal reference frames” (Flash and Sejnowski 2001, 656).

In broad strokes, two major characteristics of the computational picture of motor control emerge. First, motor control is understood as the selection and actualization of a particular set of degrees of freedom appropriate for the movement to be executed. While such a construal in itself is not incompatible with a dynamical approach, the computational account regards it as being realized through distinct and discrete cognitive subroutines. In contrast, the dynamical model treats it as a continuous manifold of coupled interactions between the components of the cognitive system. Second, computational accounts presuppose the various operations that constitute motor control take place over representations of the body and its sensorimotor states. Thelen et al.’s dynamical model, on the other hand, eschews all talk of representations, and instead regards neural activity accompanying the behaviour of motor control elements as the mechanisms used to carry out cognitive operations. Although such an explanatory strategy encounters some difficulties when it comes to accounting for aspects of motor control that involve memory and planning, as the dynamical camp itself acknowledges, they are not insurmountable. The capacity of neurons and neural populations to encode and store information about causal regularities and predict future activity on the basis of reinforced neural activity has steadily been gaining acceptance as a plausible alternative to representation-heavy explanatory frameworks.

An important contrast between computational and dynamical models of motor control—and of cognition in general—lies in their respective treatments of temporality. In dynamical systems, time is a substantive causal variable, whereas in computational systems it is not. Computational explanations regard time as a background structure; when they make mention of time, it is mainly to specify the actual or expected duration of an operation, or the rate at which it takes place. As such, the temporal parameters of a computational process are such that they indicate its extension or distribution over time. On the other hand, because dynamical accounts track the state evolution of a system—a process that is necessarily temporally extended—information regarding the activity or coordinates of the system’s elements at any given point in time is indispensable. Thus, the temporal parameters of computational models are static, while those of dynamical ones are fluid.

The novelty and significance of Thelen et al.’s dynamical model lies in the fact that its explanatory toolkit does not make use of representations. Instead, it expresses the behaviour of the variables responsible for the A-not-B error by quantifying them into

differential equations. Using these equations to create a computer model of cognitive processing resulted in a successful simulation of the A-not-B error, which was sensitive to the effects of age, repeated reaching, and spontaneous mistakes (Thelen et al. 2001). As the A-not-B error is an exemplar of behaviour that is explanatorily intractable, the success of the dynamical model in accounting for it is taken to indicate that forms of cognitive processing that are less unyielding are well within its ken. Consequently, Thelen et al.'s dynamical model stands as a prototype of how cognition can be approached dynamically. Its epistemic significance is that it sets the stage for *understanding* cognition in non-computational and non-representational terms. However, the dynamical model also brings a substantive ontological implication in its wake: it demonstrates that cognitive processing arises as the state evolution of an embodied cognitive system, i.e., that cognition is not the result of sensory, motor, and neural routines that can be regarded in isolation from each other, but has a more holistic aetiology.

As its proponents themselves point out, an important consequence that arises out of the dynamical model's organizational principles is that it is not confined to any particular type of nervous system, and thus can be used to account for intelligent behaviour in non-human species. In applying the dynamical model to non-humans, the first question to be asked pertains to the constituents of their respective cognitive systems. That is to say, the neural and corporeal elements that are non-trivially involved in processing information and generating adaptive behaviour must first be identified. These variables must then be incorporated into the differential equations that are to be used to quantify the organism's cognitive state evolution.

A dynamical approach is well suited to octopus cognition, which is markedly distributed throughout its body and of which the non-computational physical activity of the arm musculature is an indispensable component of motor control. As has been discussed earlier, motor control involves generating commands that specify the patterns of muscular activations that will bring about a desired movement. That is to say, motor commands must specify the spatial parameters an effector is to occupy over a given period of time. Doing so requires information about the actual and target coordinates of the body or the effectors concerned. In vertebrates, this is provided by the proprioceptive and kinaesthetic senses that track the position and movement of the body, and a somatotopic map that enables the positions of the limbs to be relativized to the organism's body. If a representation-using framework is to be followed, these mechanisms are what make the construction of an internal model of the motor system possible.

However, the octopus is a different case altogether. Without the benefit of internal proprioceptive points of reference, formulating and transmitting motor commands that explicitly specify which muscles to activate would have been an insurmountable task had motor control been solely the responsibility of the brain. How, then, does the octopus reduce its degrees of freedom to control its arm movements, especially when it comes to behaviour that calls for strictly following a particular trajectory? Due to the lack of proprioceptive monitoring mechanisms and the extreme flexibility of the octopus, this motor control problem is extremely difficult to account for using a computational framework, as its proponents itself acknowledge (Gutfreund et al. 1996). On the other hand, a dynamical approach would fare much better. To demonstrate this, a dynamical account of *bend propagation*—the stereotypic motor pattern used by the octopus in arm extension—will be provided in what follows.

While computational accounts of octopus motor control have been formulated, they hold true only up to a certain extent, after which a dynamical explanation is the only plausible one. Paralleling its neuroanatomical substrates, the motor control schema of the octopus can be accounted for computationally, but the *realization* of actual movements cannot. In controlling goal-directed behaviour, motor commands are generated centrally and transmitted throughout the motor system. Based on the sensory input it receives, the motor centres of the brain select a motor program to activate. The motor command associated with the selected motor program contains information about the physical profile of the movement, i.e., its overall geometrical shape, direction, trajectory, and velocity. Once the arm nervous system receives this central command, it activates the appropriate stereotypic motor pattern, in which the neural activations correlated with the associated movement is encoded and stored. Stereotypy is of the utmost importance when it comes to simplifying octopus motor control, as it eliminates the need to calculate the corresponding pattern of muscle activation from scratch with every instantiation of a movement.

The directional aspect of the central command results in the adjustment of the base of the arm to be extended so that it is directly aligned with the target and the eye with which the octopus looks at the target (Byrne et al. 2006a). Due to the hydrostatic nature of its musculature, the arm extends along a straight path once activated (Sumbre et al. 2001). Thus, if the base of an arm remains properly oriented, there is little need to exert directional control over the distal portion of the arm as it extends. Muscular hydrostats—which are dynamical systems—are characterized by a constraint to keep their volume constant, so that their constituent groups undergo compensatory lengthening or shortening based on



each other's stretch or contraction (Kier and Smith 1985). This volume constraint also renders the musculature highly susceptible to the effects of water drag. Because water is much denser than air, a submerged arm encounters more resistance than an exposed arm would. As such, submersion entails increased vigour in the neuromuscular activity of the arm. Thus, the state evolution of the arm musculature consists of the coupled interactions of the individual muscle groups with respect to each other, and (albeit to a lesser extent) how they are affected by the drag forces they encounter.

To propagate a bend, the longitudinal and transverse muscle groups of the arm are activated by a wave travelling throughout the length of the appendage. The activation wave has a bell-shaped velocity profile, which is isomorphic to the geometric shape of the movement: it initially travels slowly and gradually increases speed until it reaches a peak, after which it slows down again (Gutfreund et al. 1998). The intrinsic hydrostatic properties of the arm musculature supply and structure the counterforces needed to propagate a bend, thereby ensuring that the arm extends along the correct trajectory. This way, the central motor command that initiates the movement does not have to specify all the degrees of freedom to be used in arm extension, but only those pertaining to the orientation of the base of the arm.

The indispensability of the contributions of the musculature to motor control is further confirmed in a related study (Gutfreund et al. 2006). It was discovered that, while electrical stimulation to the axial nerve cord combined with tactile stimulation to the skin or suckers successfully evokes bend propagation, electrically stimulating the axial nerve cord *alone* does not. The authors point out three features of the neural activity of the isolated nerve cord that preclude it from generating a full-arm extension. First, rather than maintaining their strength, the bursts of neural activity in response to stimulation decrease as they course through the nerve cord. Second, the electrical activity resulting from stimulation lacks the directional preference characteristic of forward propagation taking place in naturally occurring movements. Finally, due to the absence of directional parameters, the distal and proximal ends of the nerve cord could not be identified from the electrical activity of the roots and axons of the nerves that arose from stimulation. Instead, it seems that what such neural activity resembles is the activation of local reflexes. What all of this suggests is that in order to generate the neural activity correlated with a full-arm extension, the involvement of feedback from the muscles, as well as the skin and suckers, is necessary. These findings are thus taken as evidence that sensorimotor feedback is an indispensable element in controlling the propagation of the neural activation wave

accompanying arm extension, a control organization for which support was already attested to early on in morphological studies (Graziadei 1964).

Motor control of goal-directed behaviour in the octopus can be summed up in this manner. It can begin with a computational account, with the motor centres of the brain performing the first stage of reduction of degrees of freedom by selecting a particular type of movement. Once it receives this command, the arm nervous system then activates the appropriate stereotypic motor program, which specifies the pattern of neural activity that determines how the muscles are to be activated, further reducing the available degrees of freedom (Gutfreund et al. 1996). At this point, a computational explanation must give way to a dynamical one. It is through the self-structuring properties of the arm musculature that the degrees of freedom that generate the movement are actualized. In other words, ensuring that the movement remains on track—i.e., motor control—and its actual execution are not merely simultaneous but numerically identical operations.

It may have come as a surprise that after as much endorsement of the dynamical model as was provided here, the account of bend propagation in this section began by backing a computationalist explanation. If so, it is a fair charge. The strategy taken on here was to demonstrate that even though the motor control scheme of an octopus can be construed computationally, doing so does not satisfactorily account for the actual execution of its arm movements. The implication of this conclusion is that there are cognitive routines that can yield to both computational and dynamical explanations, and there are those that unequivocally require one or the other. Arm-based motor control is an example of the latter: not only is it non-algorithmic but it is non-representational as well.

A concern that arises regarding Thelen et al.'s model is that its anti-representationalism is solely epistemic. Although it provides a coherent and consistent dynamical account of motor control, it does not definitively exclude the possibility of representation use. It could be argued—perhaps convincingly—that neural activity correlated with sensorimotor and other cognitive operations actually has representational functions. On the other hand, the structure of the arm musculature is inherently dynamical, and its behaviour when activated can only be construed as state evolution. While it is conceivable that the informational states generated by the activity of the arm may be encoded into representations higher up in the cognitive system, the muscular activity itself would not be representation-using. Thus, arm-based motor control in the octopus is an example of a cognitive routine whose dynamical construal is not merely the outcome of the explanatory framework used to describe it, but corresponds to its very ontology.

### **3.6 Conclusion: Fleshed-out cognition**

The octopus is an evolved, organic instantiation of three major organizational principles that have been identified as trademarks of embodied cognition: a functionally decentralized cognitive system, cognitive subroutines which are non-representational, and control of behaviour through the state evolution of a dynamical anatomical structure. These features of octopus cognition stand as challenges to traditional ways of understanding cognition.

The octopus's unique, almost paradoxical combination of a decentralized nervous system and complex cognitive capacities demonstrates that sophisticated intelligence can arise in a neural architecture that differs and departs radically from the centralized, vertebrate-based ones to which it is usually attributed. That the behavioural and cognitive repertoire of the octopus is highly vertebrate-like carries with it an important consequence for how cognition is understood. If the cognitive architecture of the octopus gives rise to vertebrate-like intelligence despite its bearing little structural and functional resemblance to that of vertebrates, is it possible to account for octopus cognition using the same explanatory toolkit used for more familiar cognitive systems? That is to say, can the same mechanisms that are held responsible for cognition in vertebrates be found—and should we even be looking for them—in the octopus?

One such mechanism is the forward model, which is standardly invoked in accounts of motor control due to its effectiveness as an explanatory posit. However, in the octopus, extensive offloading of motor control routines to the periphery diminishes central control responsibilities in this regard, and thus undercuts the need for an internal model of the motor system. Furthermore, the absence of a comprehensive proprioceptive and somatotopic framework would compromise the accuracy and usefulness of such a model, if the octopus nervous system does indeed make use of one. In other words, the very structure and properties of the cognitive architecture of the octopus themselves are the sources of resistance toward being accounted for through the use of the traditional explanatory toolkit.

Instead, the neural and cognitive architecture of the octopus subject themselves more readily to dynamical construals, expanding the scope of quantifiable aspects of octopus cognition that can be accounted for in entirely physical terms. The state evolution of the arm musculature, which ensures that the arm keeps to its trajectory and can be compared to fine motor control, is one such process that is recruited into cognitive routines.

The role of the arm in controlling its own movement is idiosyncratic and non-redundant, in that it cannot be brought about by any neuroanatomical component other than itself. As such, peripheral motor control is evolved proof that cognitive routines can indeed be something other than computational.

While its peripheral component calls for a dynamical approach that does not require an appeal to representations, the question arises as to whether the same holds true for the entirety of octopus cognition. Interestingly, the very inaccessibility of arm-based sensorimotor operations from the brain that makes the case for dynamical cognition also serves as a reason to posit representation use in the octopus nervous system.

Although it shares motor control responsibilities with the periphery, the octopus brain is responsible for integrative and coordinative functions. One such function is consolidating information from the optic lobes and the arm nervous system with memory and other cognitive operations whose substrates are localized in the brain. The brain lacks direct access to the sensorimotor systems of the arms, and instead receives synthesized information that has been processed locally. This raises the question as to whether this information is used as representations of the arms, which enable the brain to monitor and control the arms to the extent that it does.

Furthermore, it has been demonstrated that under certain experimental conditions, octopuses appear to “override” peripheral control of the arms and exert central control over their movements (Gutnick et al. 2011; Godfrey-Smith 2013). This putative switching from peripheral to central control seems to imply that the octopus has an internal mechanism that allows it to decide when to transfer control responsibilities. Such a mechanism would have to provide the motor centres of the brain with information about the position and location of the arm concerned. Without proprioception and somatotopy, the only plausible option would be a representation.

The distribution of cognitive routines across the anatomical components of the octopus’s nervous system thus indicates that octopus cognition is a hybrid of formats. It is comprised of embodied elements of a dynamical and non-representational nature, as well as by computational and representational ones, each delegated to particular non-redundant cognitive subroutines that can be realized only within their respective substrates. Thus, the octopus demonstrates two important things about the nature of cognition. First, it is organic, evolved proof that a single cognitive system can have distinct computational and embodied components, indicating that cognition is ontologically heterogeneous. Second, cognition should not be viewed as monolithic, such that only one framework at a time should be used

to account for it. Instead, what needs to be done is to identify the cognitive routines that require a computational explanation, and those that call for an embodied one.

## **OUT OF ARMS' REACH:**

### **REPRESENTATIONS IN OCTOPUS COGNITION**

In the previous chapter, I argued that octopus cognition is ontologically heterogeneous, and as such calls for a pluralistic approach to analysing or modelling its components. While its arm-based components are dynamical and non-representational, its brain-based ones are computational and representational. As such, an account of octopus cognition calls for a framework that distinguishes between its computational and dynamical elements and applies the appropriate explanatory schemas to them.

The dynamical nature of arm-based sensorimotor routines was established in the previous chapter; here, the focus shifts to making a case for representation use in octopus cognition. This chapter presents arguments for why representations should be attributed to octopus cognition in the first place, and explores how they are realized within the cognitive system of the octopus. Taken together, this and the preceding chapter demonstrate that representational and dynamical approaches to cognition are not incompatible, and that cognitive science should adopt an ontologically and epistemically pluralistic stance towards biological cognition.

The flow of the present chapter is as follows. Section 4.1 presents an overview of how dynamical and representational approaches to cognition stand in relation to one another. Section 4.2 expounds on the heterogeneity of octopus cognition, which was introduced in the conclusion of the previous chapter. Section 4.3 explores a number of views on representations that are compatible with embodiment. This survey is a prime for the discussions in the remaining sections, which focus on the functions and features of the representational component of octopus cognition.

#### 4.1 Introduction: Dynamicism and Representationalism

Throughout the history of the study of the mind, explanatory frameworks that make use of representations—collectively referred to as *representationalism*—to account for cognition have been dominant and preferred. This is not without good reason: the representationalist toolkit comes with numerous benefits, such as versatility and systematicity, thereby allowing a vast range of cognitive activity not only to be coherently explained, but also to be reliably predicted. Representations are thus convenient and effective explanatory postulates that make for good theory. However, the fact that representations are explanatory postulates is also the source of many problems, especially with regards to their ontology. Identifying the substrates and locations of representations within the cognitive system have long been vexed philosophical and empirical issues.

Over recent decades, concerns regarding representations have arisen that have prompted cognitive science to explore other explanatory toolkits. For the most part, this has involved considerably expanding the notion of representations beyond the arbitrary and modality-independent symbolic representations advocated by early strands of traditional cognitive science. Other moves have been more radical, and have proposed abandoning the notion of representations altogether. One such approach is *dynamicism*, or the dynamicist approach to cognition. Fielded as a direct challenger to computationalism, dynamicism replaces representations with mathematical models and differential equations (courtesy of *dynamical systems theory*) that capture real-time, coupled interactions between organism-bound cognitive elements and the environment.

Dynamicism has been steadily gaining strength, both theoretically and practically. Purely non-representational dynamical explanations have been used in plausible accounts of aspects of human and machine behaviour (Thelen et al. 2001; van Gelder 1995), and robots capable of adaptive interactions with the environment have been built using models designed according to the same principles (e.g., Brooks 1991). Furthermore, the explanatory tools of dynamicism are far less ontologically problematic than representations: the relevant physical states of the agent's body and its surrounding environment are articulated through the use of differential equations that quantify their spatiotemporal parameters and causal interdependence. Thus, unlike their representational counterparts, dynamical models do not raise thorny issues regarding the localization, substrates, format, and information-bearing capacities of their explanatory mechanisms. The ontology of dynamicism promises to be more parsimonious than that of

representationalism, making it possible to describe cognition in entirely physicalist terms. This has the further consequence of providing a causal foundation with which to ground embodiment.

As embodied approaches to cognition gain ever-increasing acceptance and popularity, the differential equations of dynamicism are often recruited to provide them with a parsimonious and empirically grounded explanatory toolkit for accounting for cognitive mechanisms and processes. By positing explanatory notions other than representations, embodied dynamical models sidestep the ontological difficulties that plague their representational counterparts. Nevertheless, while dynamicism has had considerable success in demonstrating that accounts of cognition are not confined to computational or representational frameworks, it has a long way to go before it obviates all talk of representations. In large part due to its newness, dynamicism is challenged by doubts about its explanatory power and scope. Although there is no lack of robots that successfully implement dynamical and non-representational control principles, it has been noted that the tasks they are designed to carry out are monotonously simple. Dynamicists respond by acknowledging this shortcoming, and by pointing out that their position is a young one that has not yet had the time to prove itself.

However, a greater cause for concern is that dynamicism (at least in its present state) may lack the explanatory mechanisms that enable it to provide a unifying causal framework for its target phenomena, thereby compromising its predictive power (Chemero 2011). While differential equations can quantify embodied states, there is doubt over whether they can be used as bases for the descriptive, taxonomic, and predictive aspects of dynamicism. That is to say, while differential equations can accurately quantify a particular cognitive process, *C*, are they also informative as to *C*'s qualitative and ontological features? Failure to do the latter will prove to be an obstruction to categorizing cognitive phenomena, as there will be nothing with which, so to speak, to make sense of the numbers. Furthermore, while differential equations are effective when it comes to real-time cognition, there are questions as to how well they can predict future occurrences of cognitive states.

In response to this potentially destructive charge, Anthony Chemero (2011) proffers J.J. Gibson's *ecological psychology* as a unifying background theory that would endow dynamicism with considerable explanatory and predictive powers on a par with those of representationalist accounts. He argues that ecological psychology is up to such a task because it has clear and well-developed ideas on what cognition, perception, and action are and how they arise, which can fill in the theoretical gaps in dynamical cognitive models.



Thus, ecological psychology would supply descriptive claims regarding the nature of cognitive processes, which would then be quantified in dynamical terms through differential equations.

Unsurprisingly, representationalists refuse to give up without a fight—but they have been forced to reconsider their position. While representationalists retain their eponymous explanatory tool, they have long abandoned the early traditional construal of representations as modality-independent, arbitrary, or symbolic. Instead, they posit what can be referred to as *embodied representations*, whose content is fixed by the sensorimotor states experienced by an organism and registered by its cognitive system. Such an ontological overhaul has emboldened representationalists to try to regain territory lost to dynamicism. For instance, van Gelder’s account of the Watt governor (which was discussed in the previous chapter)—the very standard-bearer of dynamicism, has been subjected to a representationalist reading, albeit an embodied one (Bechtel 1998).

However, as I am endorsing the position that cognition is heterogeneous, there is no need to pit representationalism and dynamicism against each other over the same cognitive process. Rather, the aim is to demonstrate that representations of the embodied sort are plausible, viable, and intuitive explanatory notions. In other words, what is being argued for is that where cognition uses representations, these representations are embodied.

## **4.2 Octopus cognition: A heterogeneous system**

The octopus arm occupies a unique position in cognitive motor control, as it is a considerable deviation from traditional notions of how intelligent behaviour is produced. What is notable about the octopus arm is its unparalleled motor control self-sufficiency, which is afforded by the hydrostatic organization of its musculature. As discussed in Chapter 3, the state evolution of the arm musculature generates the spatial parameters required to realize a movement, information that does not need to be processed further in order to be useable in peripheral motor control routines. That is to say, the dynamical activity of the musculature is a crucial component of intelligent behaviour.

However, as is the case with many a cognitive system governed by dynamical operational principles, the octopus arm on its own is only capable of simple behaviours. The extent of arm-based cognition, when taken locally and without reference to broader cognition, goes only as far as to enable it to react to occurrent stimuli. While the octopus arm retains its capacity to produce appropriate sensorimotor responses to various forms of

stimulation even after isolation from the brain, these cannot be initiated without a sensory trigger. Thus, although the arm's contributions to motor control are indispensable and non-redundant, the movements of an isolated arm do not qualify as goal-directed behaviour. Rather, they are sensorimotor subroutines that are recruited into intelligent behaviour, which is invariably controlled from the brain.

Unlike their peripheral counterparts, brain-based cognitive routines are best described in representational terms. One major reason for this is that their memory and planning components—which involve stimulus-independent informational states—render them too complex for a dynamical explanation to account for plausibly. However, this shortcoming arises mainly because the explanatory tools of dynamicism are not *yet* developed enough to accommodate high-level cognitive processes, and may well dissolve once the paradigm has matured. Thus, making a representationalist case for brain-based octopus cognition must be founded on something more substantive than epistemic constraints; that is to say, arguments for the representational nature of brain-based cognitive routines will not be premised on the fact that they are traditionally considered representation-hungry processes. Rather, the functional organization of octopus cognition is what gives the strongest principled reason to believe that brain-based cognition is representational. In Chapter 3, the argument was introduced that, in the absence of proprioception and somatotopy, representations are what enable the octopus brain to access sensorimotor information supplied by the arms. To unpack this argument, a deeper look at representation and representing is needed.

### **4.3 Representations**

As already noted, despite their potency and usefulness, representations have not been without their fair share of problems, notably those pertaining to the representational process, and the ontology and format of representations. While there is general consensus that the functional role of representations is to *stand in* for or bear content about something else, identifying the entities that count as representations has always been a vexed issue (Grush 2001; Stufflebeam 2001; Barsalou 1999). However, the present context makes the task a little less onerous. The cognitive system of the octopus demands that the nature of any representations it would use be of the sort that conveys interoceptive information about the physical and motor states of its body, especially its arms. Hence, traditional notions that construe representations as quasi-linguistic and modality-independent symbols that are

algorithmically manipulated are of little use here. Furthermore, the neurophysiology of the octopus suggests that representations found within it would be neurally grounded. Such representations, which will be referred to under the general term of *embodied representations*, would carry a considerable degree of isomorphism to their targets, and have their content fixed through the dynamical and real-time operations of the physical entities they correspond to.

In this section, a number of construals of representations that qualify as embodied will be presented. Importantly, many of the representations as conceptualized below are endorsed as being compatible with, or even complementary to, a dynamical approach to cognition. This survey of embodied representations is intended to help elucidate the features and functions of representations in octopus cognition.

#### 4.3.1 *Bechtel: User-dependent stand-ins*

A staunch opponent of the anti-representationalist thread within dynamicism is William Bechtel (1998; 2001). He argues that dynamical systems still make use of representations, albeit not those of the quasi-linguistic, symbolic form of traditional computationalism. He begins by calling attention to the function—as *stand-ins* for something else—and format of representations as significant and distinct aspects against which the explanatory success of dynamicism are to be assessed (Bechtel 1998). He points out that the function and format of representations are closely tied to each other: only states whose formats are appropriate to the representational process concerned are those that function as representations within that particular process. He claims that the strength of the dynamicist challenge to representations lies in its opposition to the format, and not the function of representations. To do so, he argues that, contrary to van Gelder’s landmark anti-representationalist account (1995), the states of the Watt governor nevertheless function as representations, as they stand in for information about the flywheel speed. He writes that “[the] spindle and arms [of the governor] were inserted so as to encode information about the speed in a format that could be used by the valve opening mechanism” (Bechtel 1998, 303). Bechtel notes that a strategy commonly used by dynamicists to obviate the need for representations is to posit coupling as a process by which the system gathers information about its surroundings. However, he disagrees that couplings and representations are incompatible, claiming instead that a standing-in relation can take place in the form of coupling. He thus dismisses van Gelder’s account as insufficient to rule out representational states in the Watt governor. Nevertheless, Bechtel admits that the representations used by the Watt governor are of a

“very low-level” sensory type (Bechtel 1998, 305), leading him to suppose that what dynamicists are in opposition to are higher-level representations, and not representations in general. The conclusion he draws, then, is that the dynamical and representational approaches are compatible.

Bechtel (2001) further develops the notion of minimal representations that are immune to dynamicist challenges, drawing on empirical support from cognitive neuroscience. He points out that cognitive neuroscience takes representations as a given, and argues that the representations they posit are of the same sort as those that are found in the Watt governor. Bechtel also expounds on his conception of representations to emphasize their being used within a system for the purpose of guiding behaviour. He writes that representations can be instantiated only in “systems in which there is another process (a consumer) designed to use the representation in generating its behavior” (Bechtel 2001, 337). Under his view, representations are characterized first by their being information-bearing states, and second by their susceptibility to being activated by multiple causes, not all of which are what the representation maps on to. Internal states acquire representational status due to their being used within a system that is designed to recognize such states as carriers of information. Bechtel claims that this condition is what allows any particular representation to map on to a certain target or targets, and not lose its meaningfulness by being attributed to just about anything. On the other end of the representational accuracy line, however, representations are sometimes triggered erroneously. As such, a viable theory of representation must account for misrepresentation, and this is what the multiple-cause condition addresses.

Bechtel (2001) points out that emphasis on the consumer is in line with the neuroscientific perspective, which identifies the brain as the representation user. This being the case, the next question to ask is what the vehicles of representation in the brain would be. Of the numerous candidates, “the firing rate or firing pattern of individual neurons” is what appears to be the most plausible (Bechtel 2001, 337). However this endorsement comes with a caveat: determining how and what these putative neural representations map onto proves to be an extremely problematic task. The specificity, exclusivity, and even strength with which neural activity correlates to stimuli are difficult to pin down. In fact, neural representations might not even “respond to objective features of the world...but rather their response may be relative to the current state of the organism” (Bechtel 2001, 342).

In summary, the kind of representations Bechtel believes not only to be defensible against anti-representationalism but also to be compatible with dynamicism are of the sort that are tightly correlated with their targets. The charge of arbitrariness that besets traditional notions of representations appears not to hold for the theory he develops, due to the increased importance of the contribution of the physical states of the system to the representational process that is a consequence of focusing on the user. It is the fact that an intrinsic state is used by the system as a carrier of information that imbues such a state with representational status, regardless of the format or modality in which it is realized. The dynamical processes undergone by the physical components of the system, as well as from neural activity arising as a result of the body's interactions with the external world, reflect the condition of the system, and hence are intrinsically informative states.

#### 4.3.2 Millikan: *Pushmi-pullyu* representations

Ruth Millikan (1995) posits *pushmi-pullyu* representations, a primitive type of representation that can be instantiated in simple systems, and from which more sophisticated kinds may have evolved. Millikan first distinguishes between representations that are geared towards selecting and implementing a course of action, and those that describe states of affairs. The former are referred to as *directive*, and the latter as *descriptive*. Representations that implement just one of the two functions are of little use on their own due to the limited information they carry. A directive representation guides the system to produce an appropriate response to a stimulus. However, doing so requires information about what the stimulus is like, which the directive representation lacks due to its intrinsic properties; instead, such information falls exclusively within the ken of descriptive representations. Likewise, descriptive representations capture “what is the case” (Millikan 1995, 186), but are unable to help the system to select a course of action fitting to the conditions at hand.

In order to render them useful to the cognitive system, directive and descriptive representations must be combined with each other. Furthermore, to be meaningful and informative, these combinations must be comprised of representations that are appropriate to each other: combining a descriptive representation of a normally sized red apple with one that directs the agent to swim hardly makes any sense. Millikan then argues that selection of appropriate representations calls for a combinatorial process that is inferential. As inference is a higher-level cognitive process, it requires the system implementing it to be of a sufficient degree of sophistication. Thus, even though directive and descriptive

representations each have unitary functions, they actually come with considerably high system requirements.

In contrast, pushmi-pullyu representations are *both* directive and descriptive *at the same time*. Because they carry information about what the target is like *and* how to respond to it, they obviate the need for inferential processing. Millikan gives animal signals as a paradigmatic example of pushmi-pullyu representations. These signals, such as “bird songs, rabbit thumps, and bee dances” (Millikan 1995, 186) simultaneously bear information about something, such as the location of a food source or the presence of a predator, and prescribe an appropriate course of action toward it, such as to head toward a particular direction or to take cover. Thus, the dual-functioned contents of pushmi-pullyu representations come at the price of a single substrate.

Consequently, pushmi-pullyu representations can be realized in cognitive systems that are too simple to be able to support inference-making. Millikan defines the function of pushmi-pullyu representations as “[mediating] the production of a certain kind of behavior such that it varies as a direct function of a certain variation in the environment, thus directly translating the shape of the environment into the shape of a certain kind of conforming action” (Millikan 1995, 190). Such a characterization fits in squarely with Gibson’s (1979) notion of *affordances*, or opportunities for action which are integrated into the perceptual experience of a stimulus, and Millikan suggests that the representations Gibson had in mind are actually of the pushmi-pullyu sort.

Millikan closes with an evolutionary claim. Due to the simplicity of the mechanisms required to support pushmi-pullyu representations, they are proposed to be early developments in the evolutionary history of cognition. Throughout the course of evolution, these primitive representations may have diversified and increased in complexity, eventually giving rise to specialized forms such as descriptive and directive ones.

#### 4.3.3 Haugeland: Distributed representations

In pointing out that throughout the literature, representations are standardly categorized as being language-like or logical, or image-like or iconic, John Haugeland (1991) raises the question of whether *distributed representations* constitute a proper genus. On his view, the distinctions between the genera should be based on representational content. Again, the scheme in which the process of representation is instantiated is crucial to determining what counts as representational content; that is to say, the nature of a representational process determines the format of information it traffics in. Thus, logical representations are

essentially those “characterized by a generative compositional semantics,” while iconic ones are those that “represent their contents isomorphically,” however isomorphism is construed (Haugeland 1991, 175). What, then, is the distinguishing content of distributed representations?

As suggested by its name, the content of a distributed representation is spread out across all the elements of its vehicle, such that each element non-redundantly represents a component or portion of the overall content. This being the case, it follows quite naturally that the most plausible candidates for distributed representations come in the form of *connectionist neural nets*. Haugeland pinpoints two such choices: *neural activation patterns*, and *connection weight patterns*. Due to their temporal profiles, it is believed that activation patterns and connection weight patterns represent “occurrent and episodic states” and “long-term functionality or competence,” respectively (Haugeland 1991, 199). Activation patterns are transient, as their changes are correlated with real-time system states; on the other hand, connection weight patterns remain constant over longer periods of time and undergo change more slowly, as they are associated with learning and skill development.

The sensitivity of activation and connection weight patterns to the occurrent states and state evolution of the system they are found in arises due to the fact that their function is to monitor such physical conditions for the use of control operations or routines. If these neural states are to be considered representational vehicles, it can be said that their content is encoded through dynamical processes involving the body and its interactions with the environment. Consequently, the body and the world are substantive and non-trivial contributors to the information-bearing properties of such representations, thereby qualifying them as embodied representations.

#### 4.3.4 Barsalou: *Perceptual symbols*

In a largely successful endeavour to debunk the notion that “cognitive representations are inherently nonperceptual,” i.e., are disembodied or what he describes as *amodal*, Lawrence Barsalou (1999, 577) puts forward a comprehensive and detailed theory of *perceptual symbol systems* that offers an account of how perceptual states contribute to the formation of symbolic representations. The theory endeavours to demonstrate a number of things—for instance, that perceptual symbols are on a par with what he refers to as *amodal symbols* (which have been stripped of their perceptual content and transduced into quasi-linguistic representations) posited by some traditional views, or that perceptual symbols constitute a

fully functional conceptual system. It also aims to establish that representations are embodied, and that perception and cognition are implemented by the same mechanisms; these claims are what are of interest for our present purposes.

A perceptual symbol is defined as “a record of the neural activation that arises during perception” (Barsalou 1999, 583). Because they are generated through neural activity in sensory and motor areas of the brain that accompany perceptual states, perceptual symbols are embodied representations. It is important to note that a perceptual state consists primarily of “an unconscious neural representation of physical input” (Barsalou 1999, 577), but may also be accompanied by associated conscious experience. Selective attention filters out aspects of an occurrent perceptual state for storage as a long-term perceptual memory, which upon retrieval functions as a representation of a particular aspect of the world—or in other words, as a symbol. Like amodal symbols, perceptual symbols can be manipulated and combined into increasingly complex representations.

Because they acquire their content through perceptual states, perceptual symbols are susceptible to doubts as to whether their activation is causally dependent on occurrent stimulation. The answer is that, just like amodal symbolic representations, they can be activated in the absence of stimuli because they can be stored as retrievable memories. Furthermore, the sharing neural mechanisms between perception and cognition entails that perceptual symbols can be activated through multiple pathways. That is to say, activating perceptual symbols can engage the relevant perceptual systems as effectively as actual sensory stimulation.

In contrast to amodal symbols, perceptual symbols are *modality-dependent* and *analogical*, in that “they are represented in the same systems as the perceptual states that produced them” and thus the structure of such a representation “corresponds...to the perceptual state that produced it,” respectively (Barsalou 1999, 578). Perceptual symbols, thus, excellently demonstrate how representations can have embodied grounding. Importantly, Barsalou points out that there is considerable empirical data from neuroscience and psychology in direct support of this view, in contrast to the mainly theoretical and indirect evidence for amodal symbolic representations. Because perceptual symbols originate from perceptual systems, he argues that the problems plaguing amodal symbolic representations—notably the lack of empirical evidence to substantiate them, how transduction takes place, the arbitrariness of symbols, and how they acquire meaning—are avoided. Furthermore, the modality-dependence of perceptual symbols makes the task of determining where they can be found less onerous. Neuroscientific



research has demonstrated that damage to a sensorimotor area of the brain results in correlated impairment to cognitive processes that draw on that particular area. Barsalou takes these findings as evidence that the neural substrates of perceptual symbols are found within the brain regions associated with their respective modalities, and are not confined to a particular area as suggested by traditional views.

Like Millikan, Barsalou spells out evolutionary implications of construing representations as perceptual symbols. He claims that “[not] only do perceptual symbol systems offer a more parsimonious account of how intelligence evolved, they also establish continuity with nonhuman animals” (Barsalou 1999, 606), the latter being eliminated under traditional conceptions of representations as quasi-linguistic. In addition to perceptual systems, attention and memory recruit the same cognitive pathways used for the formation and use of perceptual symbols, thus allowing animals endowed with such capacities to qualify as representation users. In turn, positing representation use in animals endows them with cognitive status that qualifies their behaviour as genuinely intelligent and adaptive.

#### 4.3.5 *Grush: The Emulation Theory of Representation*

Rick Grush (2001; 2004) construes representations as *emulators*, i.e., entities that mimic the input-output sequence of a system such that they provide duplicates of sensory feedback to the system and allow it to respond the way it would to the actual stimuli. Like most of its counterparts, the *emulation theory of representation* holds representation to be a standing-in relationship, and attributes representational status on the basis of whether an element is used as an information bearer by a system. He begins by making an important distinction between *presentations* and *representations*, which is critical to properly understanding what an emulator is (Grush 2001). What sets them apart from each other is the way by which their causal dependence on their targets gives rise to their information-bearing properties.

Presentations, of which Grush (2001) considers sensory states to be paradigmatic, are tightly coupled to their targets, such that they can only convey information about occurrent stimuli. As such, presentations are *online* information-bearing states. Representations, on the other hand, function as “a model of the target which is used off-line to try out possible actions, so that their likely consequences can be assessed without having to actually try those actions” (Grush 2001, 351). Retaining their information-bearing properties even though they are decoupled from their targets thus allows representations to present information counterfactually. This sets representation-using

systems—with which Grush (2001) equates genuinely cognitive systems—apart from systems whose behaviour, regardless of complexity, is merely the result of reactions to occurrent stimuli.

The notion of emulation is built on the foundations of *closed-loop* control architectures. In contrast to *open-loop* systems, wherein a controller issues a command sequence based solely on input about the system's current state to bring it into a goal state, a closed-loop control organization incorporates real-time feedback to update its command sequence and modify it as needed. Thus, the command sequence used by a closed-loop system is formulated, at least in part, alongside the system's state evolution. As efficient as they are, closed-loops systems are not without problems, such as susceptibility to feedback delay if the sensory mechanisms are not perfectly calibrated. Furthermore, the use of feedback to continually update the system implies that closed-loop architectures call for constant coupling with the environment, or what is known as *obligatory action*.

Grush (2001) notes that feedback delay and obligatory action—but more so the latter—raise problems for cognitive models that are based on closed-loop systems. The controller of a closed-loop system, which is taken to correspond to cognitive processing, must remain coupled to the environment and to the system's effectors in order to function. However, he points out that this is far from the case with humans, whose cognitive activities can take place solely as mental operations, independently of real-time interaction with cognitive artefacts or with present stimuli. Human cognitive systems—and cognitive systems in general, for that matter—are neither constrained nor confined to obligatory action; this decouplability is due to their use of representations, which supply the system with information about a target, which as such does not need to be present.

Grush (2001) attributes the considerable independence of cognitive processing from occurrent stimuli to the functional organization of cognitive systems. Cognitive systems are construed as being comprised of a *controller*, which generates command sequences based on system information sourced from sensory mechanisms, and an *emulator*, which mimics the output of the controller. Two copies are made of the output issued by the controller, one of which is sent to the output-producing subsystems, and the other to the emulator. In addition to being identical in content, both copies are identical with regards to their causal efficacy and function; in other words, the system can operate based on information sourced either from actual sensory input or from the *emulator copy* of sensory input. When the latter is the case, the emulator stands in for or represents the state of the system.

While Grush (2001) admits that identifying exactly what states serve as representational vehicles has always been a vexed problem, he maintains that cashing representations out as emulators entails that representations are present within the human nervous system. One of the examples he presents to make his case is empirical evidence towards emulator use in the musculoskeletal system (Grush 2001; 2004). The presence of musculoskeletal emulators—which are thought to be found in the cerebellum (Grush 2004)—is suggested by the fact that the execution of voluntary movements is much faster than the time it takes to distribute proprioceptive feedback, and evidence that corrections are made to the motor program while it is being carried out. Grush (2001) points out that these findings appear to be inconsistent. Real-time proprioceptive feedback is supposed to be responsible for updating the motor command sequence, but how can it do so if it is slower than the actual movement? He suggests that the temporal discrepancy is resolved because the motor control system uses an emulator that informs it of the intended trajectory. Thus, the necessary adjustments made to the movement are based on the system's response to the emulation and not to actual proprioceptive feedback.

The emulation theory of representation has also been used to account for motor imagery (Grush 2004). Empirical evidence strongly suggests that there is considerable overlap between the neural substrates that produce both motor imagery and overt motor actions. While they both involve many of the same brain areas responsible for motor control, it seems that the crucial difference between them is that motor imagery on its own does not activate the primary motor cortex, which controls execution of movement. Grush (2004) takes this to imply that the emulator copy may be formed before the relevant neural input reaches the primary motor cortex. It is proposed that motor imagery involves the motor areas of the brain engaging an emulator of the body, thereby generating “faux proprioception and kinesthesia” (Grush 2004, 385). When an actual movement is executed, the muscles and sensors within the effector concerned produce proprioceptive and kinematic signals, which are transmitted back to the motor control centres. The motor control centres then use this input to refine the motor commands they issue. In the case of motor imagery, motor commands are received by the emulator, which then gives off responses identical to those that would have been produced by the actual effectors. Thus, the emulator generates signals that can be used by the motor control centres in the same way as actual proprioceptive and kinematic input.

In addition to their information-bearing capacities, emulators also have a motor control function. In the same way that it ensures that the controller continues to receive

information about the sensorimotor systems, the emulator also maintains the command sequence from the controller to the effectors in the event of decoupling. If the causal connection is interrupted, the emulator receives the motor commands from the controller, and generates a copy of them not unlike that for sensorimotor information. It is this emulator copy of the command sequence that the effectors access if they fail to receive them directly from the controller.

The precision of motor control based on the emulator copy depends on the emulator's *articulation*, or decomposition into elements that correspond to distinct components of the representational target (Grush 2001). Depending on how sharply distinguished they are, emulator *articulants* can be individually manipulated in order to focus on the control of particular elements. Thus, when the controller formulates motor commands on the basis of a well-articulated emulator, it need only issue a command sequence directed towards the concerned section. After receiving this command sequence, the emulator can then activate the respective effector.

In summary, the idea behind emulators is that they acquire their content through neural encoding of signals arising from the body in action, and so count among embodied representations. However, as is the case with their traditional counterparts, they enable the cognitive system to decouple from the environment, or even the body itself, without compromising its processing and control routines. Thus, emulators differ from traditional symbolic representations in that they are neither arbitrary nor modality-independent, but have stimulus-independent information bearing properties in common with them.

#### **4.4 Representations in the octopus brain**

Arguments for the dynamical, non-representational nature of the arm-based components of octopus cognition have been presented in the previous chapter. Here, the focus falls on brain-based cognitive routines. This section makes a case for why brain-based cognition warrants a representational account, and explores the type of representations that it calls for.

In the vast majority of biological and artificial cognitive systems capable of independent movement, proprioception or a functional counterpart of it is a vital component of motor control, which necessitates updated information and constant monitoring of the position of the body and its parts. The octopus, however, is a striking exception to this motor control architecture. Although the spatial details of the octopus's arm movements

are supplied peripherally, the role of the brain in motor control can neither be dismissed nor overridden.

While central motor commands are not sufficiently fine-grained to control arm movements entirely from the brain, they are specific enough for transmission to the appropriate set of adjacent arms. Likewise, the peripheral information that reaches the brain is impoverished in terms of its proprioceptive component, but is robust enough to update central motor commands. While the information exchange between the brain and the arms leaves out proprioception, it does not entail that octopus motor control takes place without a way of monitoring the effectors. How, then, is octopus motor control successful without the benefit of robust proprioception? The only plausible option is the use of representations.

It has been demonstrated that in the absence of proprioception and somatotopy, octopuses are able to exert *exteroceptive* control over their movements. Exteroception involves the subject experiencing its own body or a part of it as an external object, in contrast to *interoceptive* experience, which is immediate and coming from an internal perspective. Exteroceptive perception is usually visual, and a common example of an exteroceptive perceptual state is looking at one's own hand. Here, the hand is not experienced internally, but as an object that is external to the visual system. Because of the external direction of exteroceptive states, information sourced through them is held to be encoded in the form of representations (Goldman 2012). Thus, exteroceptive motor control involves representations of the body in action.

Peter Godfrey-Smith writes that while their arms are “curiously divorced” (quoting Hanlon and Messenger 1996) from the brain, “octopuses can exert a significant degree of central control over their arms when they need to” (Godfrey-Smith 2013, 8). In a study conducted to determine whether octopuses can integrate visual input with peripheral proprioceptive information in order “to control goal-directed complex movements” (Gutnick et al. 2011, 460), subjects were tasked with retrieving food from a maze. The test conditions were such that they unequivocally demonstrated that the octopuses could use only visual input, and not chemical or tactile information, to successfully complete the task. The maze was designed to ensure that while the octopuses could use stereotypic movements such as extension and probing, reaching the reward required their arms to enter into positions not typically used under natural conditions. The task itself thus demanded a degree of precision that could be brought about only through visual guidance, which indicates central motor control: feed-forward control, or the use of pre-planned motor

commands, was ruled out as unlikely, due to the exploratory “‘crawling and probing’ nature of the search movements” (Gutnick et al. 2011, 462).

The integration of visual information with motor commands was interpreted as indicative of central control over the arm as it executed the retrieval task. These findings suggest that the brain and the arm nervous system are capable of an online exchange of information about the position and location of the arm, which is significant given “the lack of somatotopic representation of the body in the higher motor centers as well as the inability to elicit single-arm responses in stimulation experiments” (Gutnick et al. 2011, 462). Movements of such precision are not unheard of in the octopus: much of its behavioural repertoire is comprised of actions that demand fine movements, such as stacking and carrying around halved coconut shells to use as portable shelters, and using their arm tips to cleanly pick the flesh of crabs apart from their shells. These factors make the octopus a puzzling, almost counter-intuitive, case in motor control: it is able to execute complex movements that call for precise and detailed control, without the benefit of central proprioceptive information and somatotopy.

A similar control schema is attested in the well-documented case of Ian Waterman (Cole and Paillard 1998; McNeill et al. 2010), who had to relearn how to move after losing all proprioception from the neck down. As a consequence of a serious viral infection, Waterman’s nervous system was compromised in a severe case of *deafferentation*, a condition in which information from the body is unable to reach the brain due to damage to neural pathways. After being paralysed for several months, Waterman *decided* that he had to regain his capacity for movement—which he did, through an arduous process of consciously controlling every single movement through the use of conscious visual direction. (This will be discussed in more detail in Chapter 6.) Waterman himself has stated that he has no internal experience of his body; instead, his experience of it is as a visual object devoid of any other sensory connection to himself.

Both the Gutnick et al. study and the Waterman case are examples of exteroceptive motor control, which points to representation use. In both cases, subjects are considerably deprived of proprioceptive access to their effectors, but manage to control their movements through visual guidance. This suggests that the cognitive system employs a mechanism that allows for a causal connection between visual processors and motor execution routines. Such a mechanism would have to access both the information-bearing and the effector systems even when the connections between them are damaged or interrupted. Following

the discussions in the previous section, representations are the type of mechanism that fit this bill perfectly.

Once it is accepted that the cognitive system of the octopus uses somatomotor representations, the next step to take is to explore what they are like. These representations must be up to the challenge of conveying sensorimotor information to a neural structure that is not anatomically equipped to accommodate it in its original density or format. As their substrates transmit highly processed information to the brain (Hochner 2004), the content of these representations can be best described as the “finished product” of consolidated input from the millions of sensory and muscular receptors within the arm of origin. They would thus provide a high-level overview of the overall physical condition of the arm, i.e., its shape, stretch, position, and state of stimulation. Furthermore, the neural requirements for extracting and using information from these representations must be well within the capacity of the octopus brain.

At this point, an analogy to image processing software may be helpful. On the one hand, powerful software can break down an image into a very large number of pixels, each of which bears information about colour and texture. This decomposition makes it possible to edit the image at the level of individual or selected groups of pixels. However, the complexity of such a program comes with heavy demands on the processing capacity of the device implementing it. On the other hand, a less sophisticated version of the software is unable to access individual pixels, but can process and work with the image only at the level of shapes and blocks of colour. While its simpler analytical capacities require lighter system requirements than its high-resolution counterpart, they also limit the extent to which the software can manipulate images. This weaker software can be compared to how somatomotor representations of the arms are accessed and used by the octopus’s brain-based cognitive routines.

The octopus’s somatomotor representations must have access to low-level proprioceptive and sensory input, yet do not need to convey information about which individual receptors—which correspond to the aforesaid pixels—it originates from. This information constraint allows the location of their substrates to be narrowed down to an area that allows them direct access to the sensorimotor receptors in the arms, while enabling them to integrate this input to the extent that its individual source receptors can no longer be distinguished. This makes the interbrachial commissure, which interconnects the arms with each other and with the brain, the most plausible neuroanatomical area where the substrates of somatomotor representations can be found. Nevertheless, pinpointing the

exact physical location of representations is a task that need not be delved into at present. All that is of consequence is that they are found somewhere within the nervous system where they can consolidate sensorimotor input into information about the overall state of the arm in real time.

As mentioned earlier in this chapter, the representations within the octopus nervous system are of the embodied sort, with neurons and neural activity serving as their vehicles. Positing a neural format of representations in the octopus is the most parsimonious and empirically plausible move to make, as far as representation attribution is concerned. The role of representations in octopus cognition requires only that they bear information about the sensorimotor states of the arms, which is encoded in the form of directly correlated and immediate neural signals. The question, thus, is whether this neural activity is further recruited by higher level cognitive subroutines that fix the content of representations, as in the case of perceptual symbols, or whether it already has representational status at the level of implementation (i.e., distributed representations). The former is what appears to be the case in the octopus.

Under a distributed construal, the aggregated activity of all the discrete neural elements correlated with a particular sensorimotor state is treated by the user system as the representation. This implies that the user system has access to all the constituent elements of sensorimotor operations, which in the case of the octopus arm are the sensory and muscular receptors. Now, in the octopus, it is brain-based cognition (or the brain, for ease of reference) that counts as the user system—one which has no direct access to the low-level processors of the arm. Because of this lack of access, it cannot be that the total neural activity within the arm is what the brain uses as a representation. Hence, the representations used to bridge the gap between the brain and the periphery cannot be of the distributed sort. Instead, the representations used by the octopus brain are akin to perceptual symbols and not the neural activity itself. The content of these symbols is fixed through the real-time neural activity correlated with sensorimotor states.

Representations in octopus cognition also exhibit similarities to emulators, which ensure continued causal connection between the controller and the effector systems in the event that they become decoupled from each other. In a way, the brain and the arm nervous system are partially decoupled, due to the scantness of the neural connections and the ensuing exchange of information between them. By providing the brain with copies of the actual sensorimotor states of the arms, somatomotor representations enable it to formulate



motor commands in response to stimuli generated from a subsystem to which it has minimal direct interoceptive access.

However, octopus representations cannot be expected to be as clearly-articulated as their vertebrate counterparts are, due to the octopus's lack of a skeleton and other internal proprioceptive markers. Because the articulation of the components of an octopus somatomotor representation is considerably unpronounced, they cannot be used on their own to control arm movements. While the octopus brain can generate motor commands on the basis of representations, the command sequence is not fine-grained enough to direct precise movements of specific segments of the arm. Instead, the dynamical muscular activity of the activated arm supplements centrally issued motor commands in order to realize the movement.

#### *4.4.1 Summary: Representations in octopus cognition*

At this point, it is possible to draw up a full picture of what representations in octopus cognition can be expected to be like. These representations are first and foremost embodied, in that they acquire their content through neural signals immediately correlated with sensorimotor activity, making them similar to Haugeland's distributed representations. Their main role is to serve as a causal link between the central and peripheral components of the octopus's cognitive system, enabling the brain to internally monitor the animal's overall state, and to generate and transmit appropriate motor commands in response to environmental conditions without direct control over the effector system of the arms. As such, their content is mainly—if not exclusively—sensorimotor.

Octopus representations stand in for peripheral sensorimotor states, and are used by central cognitive routines, notably those with monitoring and control functions, thereby satisfying Bechtel's requirement that representations necessitate a user or a consumer system. The role they play within the octopus' cognitive system entail the following: (1) their substrates must have direct access to both the central and the peripheral components of the nervous system, (2) their format is one that both brain-based and arm-based cognitive routines can access without the need for further processing, (3) they carry descriptive information about the real-time state evolution of the octopus's arms, and (4) they convey directive information, in the form of motor commands. Octopus representations acquire their eponymous properties—which are similar to those put forward by Millikan and Grush—by duplicating sensorimotor information from the periphery and receiving the command sequence from the brain, thus allowing either neuroanatomical structure access

to the output generated from the other in the absence of direct causal connections between them.

#### **4.5 Conclusion: Hybrid cognition**

The octopus is a unique organism, in that it is endowed with cognitive processing nexuses that implement dissimilar formats of cognition, and whose substrates coincide with cleanly demarcated neuroanatomical structures. There are three morals that can be learned from this story: that plurality with regards to biological cognition should be embraced, that representations can be dependent on the body, and that the representationalist, dynamicist, and embodiment theses are compatible and even complementary.

Already an evolutionary marvel, the octopus is made even more remarkable by its being a biological instantiation of a cognitive system with distinct and heterogeneous elements. That octopus cognition divides into representational and purely dynamical, non-redundant and non-overlapping components is resounding support for the hypothesis that biological cognition does not come in only one, representational, format (van Gelder 1995; Clark and Toribio 1994). The evidentiary impact of a biological system with a clearly dynamical component comes across as stronger than that of an artificial system constructed using dynamical operational principles. Whereas the latter demonstrates that cognition *can* be construed non-representationally, an evolved cognitive system with an inherently dynamical nature asserts that biological cognition actually is sometimes instantiated in such a format. Thus, there are some instances in which cognition can be construed representationally, but for others, only a dynamical approach will do.

However, a caveat must be issued at this point: the heterogeneity of biological cognition does not entail that the different formats it can come in are always on a par with regards to the sophistication of cognition that they permit. So far, dynamicist approaches have been successful in accounting for simple or minimally cognitive behaviour, a fact that is reflected in the arm-based components of octopus cognition. Proponents of dynamicism have held their fort by arguing that all that is needed is for their paradigm to mature enough to ascend the explanatory throne, or by pushing back the lower limits of cognitive behaviour to admit rudimentary behaviours into the cognitive fold. They may be right to do so, but it remains the fact that it is possible that cognitive sophistication beyond a certain degree *necessitates* representations, and cannot be accounted for in exclusively dynamical terms.

The second conclusion, regarding the dependence of representations on the body, is evidence against modality-independent and arbitrary symbolic representations of the cognitivist sort, i.e. those that have been stripped of their perceptual features and rendered quasi-linguistic. While sophisticated cognition may indeed require representations, it does not entail that representation use downplays the contributions of the body to cognition. In an octopus, one of the primary functions of representations is to supply the brain with sensory and proprioceptive information, which are essential to motor control and hence to cognitive behaviour. It is thus of utmost importance that the content of these representations supplies reliable and constantly updated information about the state of the body. Furthermore, the use of representations in motor control requires that they are in constant causal contact with the effectors. Thus, the sensorimotor representations used by the octopus brain must be coupled to their sources of content, thereby qualifying them as embodied representations. These representations require uninterrupted coupling with the sensory and motor mechanisms to ensure accuracy of their content, and are used as stand-ins by the brain for information from these mechanisms that it has no direct access to.

The content of the octopus's sensorimotor representations is set by real-time coupled interactions between the environment and the various components of the neuromuscular system of the arm, that is to say by embodied dynamical processes. As argued previously, dynamical muscular activity is an irreplaceable cognitive subroutine, and so information generated this way forms a vital part of the content of representations. It must be noted that although dynamical and embodied operations contribute to the formation of representations, they do not overstep their substrates or impinge on each other's functions. This equitable distribution of cognitive territory puts the octopus forward as an example of a system in which the common tactics of pitting representationalism, dynamicism, and embodiment against each other as being incompatible, reducible from one to another, or redundant, with the objective of hoisting one thesis as dominant over the others, is simply imprudent. The harmonious co-existence of dissimilar formats of cognition within the octopus is evidence that these theses need not compete against each other over the same cognitive systems. Instead, the course of action to take is identifying which principles—representational, dynamical, or hybrid—are reflected by any given cognitive system, and to what extent.

## **AUTONOMY, OTTO, AND OCTOS:**

### **COGNITIVE AGENCY, SINGLE AGENCY, AND THE OCTOPUS**

The previous chapters jointly demonstrate that the cognitive system of the octopus decomposes into distinct, non-redundant components whose formats and functional responsibilities coincide with their respective neuroanatomical substrates. Of particular interest is the strict localization of peripheral sensorimotor processing and control responsibilities, a feature that is evidenced by amputated arms' almost complete retention of their neural and motor functions. This functional autonomy—and the very functions themselves—stand as principled reasons to consider the octopus arm as a self-contained cognitive system, albeit a rudimentary one.

A notion that has prevailed throughout the study of cognition is that cognitive systems are to be individuated on the basis of cognitive agents. As cognitive science has focused largely on vertebrates, another commitment has arisen as a consequence of agent-based individuation: the claim that for any one cognitive organism, there is only one agent. However, if octopus arms are self-contained or autonomous cognitive systems, maintaining either one of these claims leads to conflict with the other. This chapter investigates how these two notions, which are not only received views in cognitive science, but are jointly accepted due to their causal and nomological interconnectedness, are rendered incompatible when applied to the octopus.

## 5.1 Introduction: Systems and subsystems

Before anything else, some terminological disambiguation must first be set in place. While the entire thesis makes frequent mention of cognitive systems, the discussions within the present chapter examine them within a very particular context. As such, precise terminology that reflects a specific treatment of cognitive systems is needed. In particular, what are of interest here are biological structures with considerable anatomical autonomy, and which carry out cognitive operations.

First and foremost, a *cognitive system* has been defined as an “integrated, adaptive [system] able to perform a myriad of perceptual, motor, and problem solving tasks” (Eliasmith 2013, 2), or as an “integrated collection of capacities and mechanisms that causally [contribute] to the production of cognitive phenomena” (Rupert 2009, 7). That is to say, cognitive systems are those that carry out cognitive tasks, or operations that process information in order to generate appropriate output in response to the conditions at hand (Davies and Michaelian 2016). Traditional construals consider representation use to be the defining feature of cognitive systems, in contrast to functionally comparable structures whose behavioural output is produced as mere reactions to occurrent stimulation (Sterelny 1995; Adams and Aizawa 2010). However, the previous chapters have presented reasons to accept that certain types of cognitive processing can be carried out by a thoroughly dynamical and non-representational system.

The complexity of a cognitive system depends on the number of tasks that it is capable of supporting and executing, synchronously or diachronically. Importantly, when a cognitive system exhibits great complexity—such as the human nervous system—it is common to take a modular approach towards it. Indeed, such an explanatory tactic is commonplace within the neurosciences, which often seek to identify the physical areas of the brain associated with certain cognitive tasks (Davies and Michaelian 2016). When examining highly sophisticated cognitive systems, for ease of reference they are usually decomposed into idiosyncratic *subsystems*, every one of which is dedicated to a particular cognitive task or routine.

A modular decomposition of a nervous system into distinct cognitive subsystems hinges on identifying the neural elements that are causally relevant and self-sufficient at performing their respective cognitive tasks. In vertebrates, although the substrates of cognitive routines are for the most part found within the brain, their execution does not require organ-wide participation. To say that the brain carries out, for instance, language processing, is true but only in a trivial sense: a more precise formulation would specify that

language processing is subserved by Wernicke's and Broca's areas, and the arcuate fasciculus. Consequently, neurological approaches to language use can focus mainly on examining the activity of these areas, which can be regarded for functional and practical purposes to make up a cognitive subsystem. Thus, demarcating between cognitive subsystems—especially those whose constituents are found mainly within the brain—entails correct identification of the correlates of various types of cognitive activity. However, this task is not always straightforward, as a single brain area may participate in different cognitive routines. For instance, Broca's area is associated with language processing, but has also been found to be involved in the recognition of actions, especially gestures (Fadiga and Craighero 2006). Conversely, a given cognitive routine may recruit dissimilar substrates across individuals. As a case in point, it has been demonstrated that bilingual individuals recruit different neural mechanisms to perform the same set of mathematical and linguistic tasks in their first and second languages (Wang et al. 2007).

There are a number of important similarities and differences between a causally self-contained and functionally autonomous cognitive system—which can be termed an *independent cognitive system* for ease of reference, and a *subsystem* of a full cognitive system. What independent cognitive systems and subsystems have in common is that they are responsible for processing information about environmental conditions, on the basis of which they generate appropriate output. Another feature they share is functional self-sufficiency: they must be able to carry out the all or almost all of their idiosyncratic processing and control responsibilities without having to recruit resources external to them. While some cognitive routines can be enhanced or made more efficient through the use of external resources, the bulk of processing responsibilities must be executed by the bare system or subsystem. (More will be said about this matter later in the chapter when *extended cognition* is discussed.)

Nevertheless, cognitive subsystems are a few functional notches below their independent system counterparts. Even though they may be non-redundantly responsible for certain cognitive subroutines, their individual output when taken in isolation contributes toward but does not fully constitute intelligent behaviour. Subsystems may also be dependent on the independent cognitive system, or on other subsystems, for their activation and direction. For instance, an octopus's fetching movement requires a central command to initiate the action, even though fine-grained motor control takes place peripherally. As has been discussed in detail in Chapter 3, in robots constructed using the subsumption

architecture, higher-layer directional commands that prompt the robot to move towards a target are informed by lower-layer ones responsible for obstacle avoidance (Brooks 1991). In biological cognition, subsystems are normally anatomically inseparable from the rest of the cognitive system or the organism itself; for instance, an excised section of the brain ceases to function neurally, much less cognitively.

Under different circumstances, there would be little need to explicitly differentiate between cognitive systems and subsystems, as the distinction is an intuitive one. However, when faced with a biological structure as atypical as the octopus arm, the distinction between subsystems and their full counterparts blurs. It goes without saying that the octopus's peripheral neural network is a *subsystem* of the nervous system, in that it is a constituent of the latter and is dedicated to specific functions. Yet, this functional specificity serves double duty as the starting point for arguments that an octopus arm is an *independent* cognitive system.

Importantly, the functions carried out by the arm pertain to perception and action, the capacities for which are the minimal requirements for cognition. Furthermore—as has already been discussed over the previous two chapters—the sensorimotor responsibilities of the arms correspond to operations that in vertebrates are brain-based and uncontroversially cognitive (Richter et al. 2015; cf. Clark 2008). In the same vein, the octopus arm meets a number of criteria for the attribution of cognitive status to a physical state or process. Robert Rupert (2009) presents a survey of these criteria, which can be condensed as follows: in order to qualify as cognitive, a state or process must be a substantive contributor towards the production of cognitive output, which cannot arise without it, and which is reflected in identification of the state or process as being an indispensable component of explanatory accounts of the cognitive output in question.

There is one further compelling reason to consider the octopus arm an independent cognitive system: its anatomical self-sufficiency. Unlike the physical substrates of cognitive subsystems in vertebrates, it is possible to isolate the arm from the rest of the animal without debilitating its neural or cognitive functions. While an amputated arm may not be able to carry out certain actions in their entirety (such as extension) without stimulation to mimic centrally issued commands, it retains all of its sensorimotor control and processing functions. The octopus arm, thus, exhibits what can be referred to as *detachability*, or the capacity of a component of a cognitive system to carry out its idiosyncratic routines even after physical separation from the rest of the system.

## 5.2 Cognitive agency

Distinguishing between behaviour that is genuinely cognitive and that which arises merely as a reaction to stimuli has long been recognized as a vexed task. Both types of behaviour involve being initiated by sensory input, and have motor output as their end product. Making clean-cut distinctions is complicated further by the numerous instances of highly complex yet non-cognitive behaviour (e.g., ants' removal of dead conspecifics from their nests, which is driven entirely by reactions to oleic acid). Much of modern approaches to the study of the mind posit representation use as the defining feature that sets cognitive input-output cycles apart from their merely reactionary or stimulus-dependent counterparts. However, relatively recent developments in cognitive science (such as the growing acceptance of dynamicism) have led to the consequence that the use of representations can no longer be regarded as the necessary and universal component of cognition. However, the underlying reason and need to posit representations as the mark of the cognitive points to a deeper fundamental feature that is an incontestable characteristic of cognition: stimulus-independent information processing.

Representations are an explanatory construct that facilitates the formulation of coherent accounts, among other phenomena, of how neurocognitive sensorimotor activity can be generated without the need to be activated by a constant inflow of sensory stimulation. Representations have been unprecedented in their effectiveness as ontological and epistemic mechanisms that make it possible for an organism to successfully navigate the environment—by responding appropriately to present conditions, and planning responses to anticipated ones—by expanding the scope of available and accessible information beyond what the senses can immediately provide. Such a capacity brings in its wake the ability to self-initiate and self-direct cognition, or at least certain types of cognitive processing. That is to say, cognitive processing does not always depend on external stimulation for its activation, updating, and flow. This stimulus-independence, in turn, leads to another construct that has long been regarded as a salient feature of cognition and hence a defining attribute of cognitive systems: *agency*.

The notion of the *cognitive agent* has long been used as the basis for individuating or demarcating the physical boundaries of cognitive systems. Associating an independent cognitive system with a cognitive agent is a notion that arises naturally from representationalism. It must be kept in mind that representations acquire their eponymous status not just by standing in for informational states, but also due to their *being used* in



this capacity by a consumer process or processes, or the psychological or neural routines whose operations require the information provided by the representations they recruit (Bechtel 2001). These consumer processes are usually those responsible for producing behavioural output, but can also be higher-level or finer-grained information processing routines. The notion of the user or consumer thus implies that the functions of a cognitive system include 1) specifying the end goals or target phenomena toward which cognitive processing is directed and 2) activating the processes required to achieve these goals. It is of the utmost importance to note that these functions are those that are characteristic and definitive of agency. Significantly, the dependence of cognition on an agent is even stronger under representationalist views with an embodied slant. In grounding the content of cognitive states in the body in action, embodied representationalism renders the cognitive system inextricable from the individual organism, and hence the agent.

Intelligent or adaptive behaviour—the output component of a cognitive system—likewise implies agency. A vital aspect of adaptive behaviour is the organism's deliberate manipulation of certain features of the environment in order to optimize its interactions with its surroundings. As such, these modifications to the external environment are carried out by the organism in reference to its own goals and physical conditions. Without this intentional aspect—which is not only another mark of agency but a sophisticated one at that—the organism's actions would merely be rearrangements of physical elements of the environment.

Another notion with a strong foothold is that of *single agency*, the claim that there can be only one cognitive agent instantiated within any given cognitive system (cf. Bayne 2010; Clark 2008; Baars 1983). The commitment to single agency arises as an empirical consequence of the centralized cognitive models that have long been favoured due to their unprecedented success at generating sophisticated intelligence, a fact that is well observed in biological cognition and has been replicated frequently in its artificial counterparts. However, single agency also has theoretical roots, in the construal of the cognitive system as an integrated processing and control nexus. In order for the agential functions of initiating and directing cognitive processing to be carried out effectively, the organizational structure of a cognitive system must be such that effector mechanisms have access to sensory input that provides comprehensive, real-time information about the external environment and the organism's internal states. Likewise, because individual effectors are responsible for executing various components of movement, which they do in response to different facets of stimuli, effector mechanisms must be highly and vigilantly coordinated.

As such, motor commands must not only be fine-grained enough to exert precise control over the diverse set of effectors, but they must also specify the features of the world that individual effectors are to act on. This requires motor control mechanisms to have access to synthesized sensory information, aspects of which it extracts for formulation into motor commands relevant to the articulation of the effectors involved.

Neither the possibility nor the plausibility of multiple agency within a single organism is looked upon favourably. The main reason for its unpopularity is that multiple agency is expected to generate inconsistent or incoherent motor actions, especially when the distinct agents lack a reliable means of information transfer between them. In the event that one agent receives information that is incomplete, or in conflict with that received by another, the commands they would issue to the effector systems run the risk of giving rise to uncoordinated behaviour. To ensure that the organism's motor actions are coherent and not potentially deleterious, the agents housed within it must be capable of synthesizing the information they receive in order to eliminate conflict and redundancies. Even though an organism's processing and control routines may be distributed across multiple functionally autonomous mechanisms with little intercommunication between them, its effector systems require comprehensive access to sensory information in order to properly delegate motor responsibilities. While information processing routines may take place independently of each other, formulating coherent motor commands requires communication and coordination between motor elements in order to determine which of them are to be activated or inhibited. Thus, because it requires comprehensive information in order to give rise to coordinated actions, the motor system in effect realizes centralized control principles—which in turn generate output that is identified as being that of a single cognitive agent (Baars 1997; 2005).

Were an organism to house multiple cognitive agents, their effectiveness at generating motor output would be significantly hampered by anatomical constraints. Where they are present, rigid skeletons entail limited degrees of freedom, reducing or altogether eliminating the possibility of anatomical redundancy, i.e., different limbs being endowed with the same capacities for movement. Furthermore, most forms of intelligent behaviour require the coordinated but non-redundant participation of multiple effectors, which is unlikely to arise if they were all receiving conflicting or disharmonized commands. However, these anatomical constraints do not apply to the octopus. Octopus morphology is such that it is *physically* possible for each of its arms to simultaneously execute a task distinct from that of the others, were they to receive the relevant motor commands to do so.

Thus, from an anatomical perspective, if there were a creature that could possibly support the motor demands of multiple cognitive agents, it would be the octopus.

### 5.3 Extended cognition: A theoretical anchor

The notion that cognition is agent-dependent is one that has been so pervasive for so long that it has become rather platitudinous. Thus, it is helpful to present a cognitive model that projects the role of the agent in renewed sharpness—ironically, by threatening to blur its boundaries. This theoretical anchor is *extended cognition*, which challenges the traditional notion that the physical underpinnings of cognition are limited to neural operations that are localized in the brain, or at most within the central nervous system. On the contrary, the premise of extended cognition is that the substrates of cognition can incorporate external physical objects or non-physical resources, the manipulation of which enables or enhances certain forms of cognitive processing.

Extended cognition was first introduced by Andy Clark and David Chalmers (1998) through the now-classic thought experiment of Otto and his notebook, by which they demonstrate the plausibility of the inclusion of external resources into the substrates of cognition. Here, they compare the cognitive routines of neurally and psychologically unimpaired Inga with those of early-stage Alzheimer's patient Otto. Both Inga and Otto, who are presumably long-term residents of New York, hear of an interesting exhibit at the Museum of Modern Art and decide they want to go. Inga takes a quick moment to recall that the MoMA is on 53<sup>rd</sup> St., and heads off. In contrast, for Otto, recollection is not as straightforward. Due to the progressing unreliability of his biological memory, he has taken to meticulously recording factual information in a notebook that he carries with him at all times and consults whenever he needs to recall something. In other words, Otto is absolutely dependent on his notebook for the propositional content of his fact-based mental states. Upon getting wind of the exhibit, Otto flips through his notebook, finds the entry that gives him instructions on how to get to the MoMA, in particular saying that the MoMA is on 53<sup>rd</sup> St., and makes his way over.

What Clark and Chalmers aim to establish is that Otto's notebook is, for all functional purposes, a replacement for his biological memory (or at least the semantic component of it). They point out that the contents of the notebook function in exactly the same way as brain-based factual beliefs do, in that they can be recruited into various propositional attitudes. They claim that the sole difference between the information in the

notebook and biological memory is that the former is stored outside Otto's organismic boundaries. To defend this position, Clark and Chalmers introduce the *parity principle*, which holds that "if a part of the world functions as a process which, were it done in the head, we would have no hesitation in recognizing as part of the cognitive process, then that part of the world is...part of the cognitive process" (Clark and Chalmers 1998, 8). In other words, the parity principle is intended to eliminate the privileged status placed by cognitive science on neural structures by allowing external, non-biological resources to be considered proper parts of cognitive routines (Clark 2008).

Clark and Chalmers (1998) view *coupling*, or the causal interdependence of the behaviour of the components of a system, as what makes it possible for external resources to become integrated into an agent's cognitive routines. To form an extended cognitive process, an external resource must be used by the agent to the extent that the cognitive process cannot be carried out in its entirety, or with the same effectiveness or efficiency, without the utilization of the external resource. Thus, it can be said that Otto is psychologically coupled to his notebook, in the sense that the content of the notebook provides information that is necessary for his forming propositional mental states based on semantic memory.

As the case of Otto demonstrates, one of the forms cognitive extension takes is incorporation of a physical object into information processing routines in order to facilitate or enhance the production of cognitive output. A common real-life example is a blind person's use of a cane, which becomes an extension of her tactile perception. As such, and especially after a short period of habitual use, the cane usually becomes "transparent," such that the agent's sensory experience is not predominated by the feel of her hand grasping it but by the tactile qualities of the surfaces of objects encountered. A similar phenomenon is reported by experienced musicians, notably those who play bowed string instruments (Sosnik et al. 2004; Davies 2003). There are abundant anecdotal reports that with time and mastery, the bow becomes an extension of the musician's right arm, so that it amplifies technical expression. In these and other cases, the tool becomes incorporated into the agent's neural pathways (Clark 2008; Menary 2010). As dependence, frequency, or proficiency in its use increases, integration into the *body schema* (the non-conscious interoceptive sensorimotor system used to monitor the body) deepens. This is due to the fact that physical manipulation of an object generates neural signals that code for the action, which are reinforced or strengthened by regular repetitions of the action.

Cognition can also be extended through the use of symbol systems, such as numbers or written language. Clark (2008) gives the example of our use of a pen and paper to multiply large numbers. While very simple arithmetic can often be done mentally without much difficulty, a problem involving three-digit multiplicands is usually too much to compute unaided (save in the cases of mathematically gifted individuals). Three-digit multiplication involves several steps, which can prove to be too demanding to keep track of mentally. Thus, most people resort to the useful tactic of solving the entire operation on paper (in the absence of a calculator, that is). Writing out mathematical operations offloads much of the information and cognitive workload involved in them—i.e., keeping track of the order in which digits are to be multiplied with one another, the numbers that must be carried over, the sums of the different addends, and so on—onto a persisting external record that readily and immediately allows the agent to monitor her progress, and which is updated in real time as the calculation proceeds. As she does not have to rely on constant mental reminders of how far she is in the calculation, so her cognitive labour is significantly reduced. This in turn frees up neurocognitive processing space for other aspects of the mathematical operation. Importantly, Clark points out that manipulation of linguistic and mathematical symbols can extend cognition for the long term. He argues that the capacities for reading, writing, and arithmetic enable humans to engage in highly complex cognitive tasks that we would not have been capable of without the assistance of these symbol systems. Thus, he considers symbol systems such as those utilized by language and mathematics to be *cognitive scaffolds* that allow for the generation of new, informative symbols that are internalized anew.

Yet another type of extended cognition takes place through the use of the body as an object (Goldman 2012), such as doing simple arithmetic using one's fingers, or tapping one's foot to keep time while playing music. In cases such as these, subroutines of the cognitive task in question are offloaded from the brain through the performance of particular actions, which are registered interoceptively through proprioceptive feedback, and—more importantly—exteroceptively through the relevant sensory systems' responses to the visual or auditory components of the action. The latter are what David Kirsh and Paul Maglio (1994) refer to as *epistemic actions*, in which bodily activity is used to produce information that is required to perform a particular cognitive task.

What the various forms of extended cognition have in common is their acknowledgement of an important distinction between the entity that carries out cognitive

processing, i.e., the cognitive agent, and the external components of cognitive processes. A concern has been raised that a consequence of extended cognition's acceptance of resources found in the external environment as proper parts of cognition is that it fails to respect organismic boundaries and so compromises the notion of personhood (Rupert 2004). However, this worry has been dismissed by Clark (2008) as unfounded. Even with acceptance that Otto's notebook is an external memory source analogous to biologically instantiated beliefs, it does not follow that "Otto" refers to the biological organism *and* the notebook. While the notebook may be part of his cognitive system, Otto remains the sole cognitive agent, in reference to which persons are individuated. Otto is the *core* component of the cognitive system that comprises him and his notebook, as the substrates of cognition that allow him to initiate and direct cognitive activity are found within his body. As such, Otto the human organism alone is the cognitive agent, which recruits external resources in order to enhance his cognitive processing.

Importantly, Clark (2008) makes an ontological assertion about the neural substrates of the cognitive agent. In response to worries that extended cognition ignores the distinctness of biological contributions to cognitive processing (Rupert 2004; Adams and Aizawa 2010), Clark reiterates the indispensability of identifying a persistent biological core. He explicitly points out that the cognitive agent is to be grounded in this biological core, and not in the mechanisms of individual cognitive processes. He writes that the individuation of cognitive agents takes place by "identifying...a reliable, easily identifiable physical nexus of perception and action, apparently driven by a persisting and modestly integrated body of goals and knowledge" (Clark 2008, 118). A little further on, he specifies that "the organism (and within the organism, the brain/[central nervous system]) remains the core and currently the most active element" (Clark 2008, 139). Following these characterizations, an extended cognitive system can thus be decomposed into 1) a persisting *core*, by which the cognitive agent is individuated, due to its containing the main substrates responsible for cognitive processing, and 2) *addenda*, or the external resources that are recruited by the agent in order to enhance cognitive processing.

Clark's take on the interrelation of the cognitive system, cognitive agent, and cognitive core can thus be condensed into the following claims. First, the substrates of an extended cognitive process can be found within the brain, in the body outside of the brain, and in the external environment. Second, the brain or the central nervous system constitutes the core of the cognitive system, as it is where the substrates of autonomous cognitive processing are localized. And third, because the cognitive core is what executes the agential

functions of initiating and directing cognition, it is the neural structure that underpins the cognitive agent.

From these characterizations, an important feature about the cognitive agent can be derived. In biological cognition, the cognitive system overlaps with the nervous system, and so can function only when the organism is intact. Accepting Clark's grounding of the cognitive agent in the central nervous system leads to the conclusion that the physical substrates of the cognitive agent do not extend past the corporeal boundaries of the organism. Furthermore, the embodied context within which Clark writes is not one that conceives of the cognitive agent as a homuncular and ontologically spooky entity, as would arise from a Cartesian reading. Instead, the agent is construed functionally, and can be parsed in terms of neural operations whose content is inextricably dependent on somatomotor and sensory states. As such, it is common practice to individuate the cognitive agent on the basis of the organism: cognition is regarded as an activity carried out by an organism, and not just by its nervous system.

#### **5.4 Agency and the octopus**

To recapitulate, two of the received views in cognitive science pertaining to how the physical boundaries of a cognitive system are demarcated rely on appeals to agency. The first of these views is that the cognitive system is individuated on the basis of an agent; hence, it will be labelled as the *cognitive agency claim*. It maintains that identifying a set of causally interconnected physical elements as a cognitive system depends on whether they are collectively self-sufficient to initiate and direct coupled sensory processing and motor control functions. The second view, which can be called the *single agency claim*, holds that a fully cognitive organism (as opposed to a minimally cognitive one whose behaviour arises mainly in response to sensory stimulation) can house only one agent. Because the single agency claim is often regarded as an empirical consequence and theoretical corollary of the cognitive agency claim, accepting the first usually entails accepting the second as well.

Joint acceptance of the cognitive agency and single agency claims results in inconsistency when applied to the octopus. That is to say, maintaining the truth of one compromises that of the other. First of all, the atypical functional and anatomical independence of the octopus arm stand as principled reasons to consider it an independent cognitive system. If these reasons are accepted, the conclusion follows that within the

octopus, there are nine full cognitive systems—each arm, and the overall nervous system. Thus, maintaining the cognitive agency claim requires a numerically distinct agent to be attributed to each cognitive system, thereby violating the single agency claim. On the other hand, retaining the single agency claim entails renouncement of the notion that cognitive systems must be individuated on the basis of an agent, i.e. the cognitive agency claim.

The question thus arises as to which of these two claims is more defensible when applied to the octopus. As the cognitive architecture of the octopus is highly atypical, the usual grounds on which they are adjudicated may not be applicable to it. To begin with, anatomy is a major contributing factor to the plausibility of the single agency claim; however, the lack of proprioceptive markers and monitoring mechanisms due to the flexibility and soft body of the octopus entail that it may not be faced with the same constraints on the structure of its cognition. That is to say, if instantiation of a single cognitive agent evolved in the octopus, it may not have been under the same conditions as those that favoured single agency in vertebrates. If such an evolutionary development were indeed the case, then housing multiple cognitive agents may not be maladaptive in the octopus, as it is in vertebrates. In other words, the octopus may not be as susceptible to incoherent behaviour as its vertebrate counterparts, were it actually endowed with multiple agents.

Furthermore, the modularization of the octopus nervous system can be proffered as instantiating an evolved functional organization by which multiple cognitive agents can be coordinated. Such a possibility is suggested by the *lateralization* (side-specific function and processing) of the octopus visual system: each eye and its corresponding optic lobe process information independently of the other, and information transfer between the eyes does not take place automatically (Byrne et al. 2002; Byrne et al. 2004; Mather 2008). As such, octopuses can have two distinct visual experiences, one for each eye. Interestingly, selection of an arm to use in a retrieval task takes place on the basis of which eye had seen the object to be grasped (Byrne et al. 2006a). Thus, it is possible for the motor commands to extend a particular arm to be triggered by the visual system on one side, without the involvement of its contralateral counterpart.

Lateralization as extensive as that of octopus vision implies that a task can be carried out without the involvement of the entire nervous system. This further suggests that an unrelated task with similar sensorimotor requirements can be carried out by the octopus at the same time, under the control of the corresponding neural components on the other side. If the octopus were capable of lateralized multi-tasking, it would make a very strong



case for multiple agency. Unfortunately, it appears that no studies investigating this matter have been carried out yet, and so the argument remains speculative. Nevertheless, lateralized visual processing and the ensuing motor command sequence strongly indicate that the octopus may be morphologically capable of supporting multiple cognitive agents.

Meanwhile, the cognitive agency claim is motivated by the arms' functional self-sufficiency. As has been discussed in previous chapters, a centrally issued motor command initiates the movement of an appropriate arm or arms, but the motor profile is determined and actuated peripherally. Coarse-grained control over the shape of the movement takes place through the selection and activation of locally stored motor programs, whereas fine-grained adjustment of the movement is carried out through sensorimotor feedback loops and dynamical muscular activity. Agency is suggested by the fact that the arms are able to autonomously process sensory information and select the motor programs appropriate to the environmental conditions currently experienced by the animal.

Such a distribution of motor control labour is suggestive of cooperation between a global, central agent that monitors the octopus's overall state, and specialized ones in charge of local sensorimotor processing and control. Given Clark's proposal that the cognitive agent is parasitic on the cognitive core, it follows that the capacities of an agent are directly correlated with the functions of its neural base. Because the central agent—whose substrates are localized in the brain—does not have direct participation in the sensorimotor operations of the arms, it can be said that its functions are not comprehensive. That is to say, the central agent has limited access to sensory information and restricted influence over motor control. Instead, much of these responsibilities are offloaded to the arm nervous system. The functional autonomy of the arms, which is highlighted by post-amputation retention of their sensorimotor capacities, is indicative of a considerable degree of self-directed processing and control. Furthermore, the axial nerve cords have been characterized as high-level integrative and processing centres (Richter et al. 2015), and as such qualify as peripheral cognitive cores. These functional and neuroanatomical features of the octopus arm are of the utmost importance, as they are redolent of the substrates of cognitive agency.

However, the question arises as to the extent to which the arms are capable of self-initiating their operations. While amputated arms' sensorimotor capacities remain relatively unimpaired, it is important to note that their activation is stimulus-dependent. Similarly, although much of the control over arm movements in intact octopuses is peripheral, central commands are required to activate them. Thus, the agential functions of

the octopus arm are likewise limited: while they are capable of self-directing their operations, they are considerably restricted with regards to self-initiated processing.

At this point, it is possible to take stock of the realization of agents within the octopus nervous system. Coinciding with its neuroanatomical divisions, agential functions are distributed between the central cognitive core, i.e., the brain, and the peripheral cores, i.e., the axial cords within the arm nervous system. However, their functions and capacities are asymmetrical. The brain-based central agent is responsible for monitoring and controlling the overall state of the animal, while arm-based peripheral agents are in charge of fine-grained sensorimotor operations. Nevertheless, both types of agents are beset by functional constraints: the central agent has limited access to sensory information and motor control, while its peripheral counterparts are dependent on the central agent for their activation. What this distribution of labour suggests is that there is a single agent whose substrates are spread across multiple cognitive cores, i.e., the brain and the individual axial nerve cords—but this decomposition holds only in an *intact* octopus. By contrast, it is amputation of the arm that brings the possibility of its independent agency to the forefront.

As has been discussed over Chapters 3 and 4 and earlier in the present one, the sensorimotor functions of the octopus arm meet the minimum criteria for full-fledged status as an independent cognitive system. Not only is the arm capable of integrating and structuring sensory information for use in motor control, but the operations localized within it—i.e., determining the spatial parameters and geometric shape required to successfully execute a movement—are uncontroversially cognitive (cf. Wolpert 1997). There are thus strong, principled reasons to consider the isolated octopus arm an independent cognitive system. Presupposing adherence to the cognitive agency claim, accepting these reasons leads to the conclusion that agency must be attributed to the octopus arm. However, it stands out that the octopus arm does not exhibit one vital causal characteristic of cognitive agency: the ability to self-initiate its operations. Thus, the cognitive agency and single agency claims cannot be jointly maintained in the octopus: one must yield to the other.

Between the cognitive agency claim and the single agency claim, it is the former whose hold becomes tenuous when applied to octopus cognition. While there are good empirical grounds to reject the single agency claim, there is also compelling evidence that the octopus actually houses only one agent. It is reasonable to suppose that there are multiple agents present within the octopus, but that they are subsumed under the central, brain-based agent when the animal is intact. That is to say, the arms retain their integrative and control functions, but their activation is causally dependent on commands from the

brain. Consequently, the central and peripheral agents in an intact octopus are coordinated with each other in such a way that they conjointly function as one agent. Another plausible indicator for single agency is goal-directed behaviour, as it calls for an integrated and comprehensive informational state, on which motor commands for coordinated actions of certain arms are based. Thus, while the applicability of the single agency claim to the octopus is uncertain at worst, it does not encounter serious empirical or theoretical complications.

On the other hand, the cognitive agency claim is compromised, regardless of whether it is applied to an intact octopus or one that has undergone amputation. While octopus arms demonstrate characteristics of independent cognitive systems, attributing agency to them appears to be imprudent due to their dependence on central activation or on occurrent stimulation. Although the arms are self-sufficient enough to self-structure sensorimotor information, they are not autonomous enough to self-initiate their operations. The octopus arm therefore stands as an example of a cognitive system that is resistant to agent-based individuation; that is to say, it is a cognitive system that neither supports nor generates an agent.

Nevertheless, it is important to note that the inapplicability of the cognitive agency claim to the octopus arm does not entail that it is false altogether. Some cognitive systems, such as Otto, are best individuated along agential lines, especially when their substrates incorporate non-biological external resources. Again, the octopus challenges a received view—this time regarding how a set of elements is demarcated as a cognitive system—not by debunking it, but by necessitating that a pluralistic stance be taken toward it.

## **5.5 Individuation of cognitive systems in the octopus**

The importance of a reliable means of individuating cognitive systems is underscored by the existence of cognitive models that hold that cognitive processing is not confined within the boundaries of the organism. When the substrates of cognition reach beyond a single biological individual to include external resources, or even other cognizing biological individuals, identification of the elements that are causally relevant to information processing routines is a vital task. A biological organism is inevitably affected by the conditions of the environment it is situated in, so there must be standards by which to distinguish between those conditions that have a substantive impact on its cognitive

operations and those that do not. Furthermore, cognitive status is not automatically bestowed on an external object that is used in order to enhance or supplement cognitive processing (Clark 2008); while writing out arithmetic operations is an example of how external resources are indispensable to a cognitive operation, it does not entail that the pen and paper used can be considered cognitive entities.

The individuation problem becomes even more pronounced when dynamical systems are concerned. It must be kept in mind that the state evolution of a dynamical system is dependent not only on how its components interact with one another, but also on how they respond individually and collectively to environmental influences. Since embodied, dynamical cognition rests on the coupled interactions of the different parts of the cognitive system and the world, it is easy to formulate a promiscuous account that unhelpfully includes too many elements as part of the cognitive process. Without a proper means of individuating cognitive systems, a physiologically vital but cognitively irrelevant element, such as the air breathed by the organism, might be wrongly identified a substrate of cognition—a move that is utterly absurd. Thus, dynamical systems necessitate a principled means of extricating elements that exert causal influence on them but do not contribute to their substantive functions.

Individuating cognitive systems along the lines of an agent is a relatively reliable and efficient means of separating the cognitive wheat from physiological and environmental chaff. This is because agent-based individuation comes with the benefit of a persisting core that serves as a reference point for identification of information-supplying and output-producing systems. However, as has just been demonstrated, not all cognitive systems can be subjected to agent attribution. How, then, are such systems to be individuated? As an alternative to agent-based accounts, Jim Davies and Kourken Michaelian (2016) propose individuating cognitive systems according to the cognitive tasks they carry out. Their *task-based approach*, as they refer to it, holds that demarcating the boundaries of a cognitive system must be done in reference to the particular cognitive routine or operation in question. A cognitive system is thereby construed as a set of causally interconnected elements responsible for executing a pre-identified task or set of tasks. Thus, the elements constituting the cognitive system are those that are immediately responsible for processing information and producing behavioural output according to specific task requirements, and without whose contributions the task cannot be carried out. Importantly, the authors point out that “identifying a cognitive system does not presuppose first identifying an agent” (Davies and Michaelian 2016, 7); in other words, an agent may be

instantiated within the cognitive system, but the composition of the cognitive system is not dependent on the set of physical elements that collectively give rise to an agent.

Thus, agent-based individuation is not well-suited to the octopus, as it entails either giving up the cognitive agency claim altogether or denying that the octopus arm is a cognitive system. Needless to say, maintaining the cognitive agency claim precludes the former option; however, available empirical evidence does not support the latter. On the other hand, these inconsistencies are sidestepped by task-based individuation of cognitive systems. As has been discussed in a number of earlier places in this thesis, the correlation between the neuroanatomical features and functional responsibilities of the octopus arm is conveniently straightforward, making for an unequivocal association of cognitive tasks with the system that idiosyncratically realizes them.

## **5.6 Conclusion: Non-agential and dynamical cognition**

This chapter presented how the octopus challenges another set of received views in cognitive science, in particular those pertaining to the notion of agency. Due to its unique neurophysiology, the octopus is an evolved example of an organism in which 1) multiple cognitive agents can be instantiated *and* 2) non-agential cognition is realized. The body plan of the octopus is such that it can possibly accommodate multiple cognitive agents without being beset by the same potentially maladaptive consequences as its vertebrate counterparts. However, whether it actually does house multiple agents is an empirical question over which there is some uncertainty. Nevertheless, the plausible answer to this question is that only one agent has causal influence over the octopus's behaviour at any given point in time. While the octopus's lateralized vision suggests that it can have two perceptual fields—which is indicative of multiple agency—the empirical findings that are available at present point to only one of them at a time being able to exert control over goal-directed behaviour.

Interestingly, the octopus also stands as an example of a cognitive system that is resistant to agent-based individuation, running counter to the widely held notion that the independence of a cognitive system depends on whether it houses an agent. The octopus arm demonstrates features attributed to independent cognitive systems, yet lacks the capacity for self-activation that is characteristic of agents. Instead, the octopus arm yields itself more readily to a non-agential, task-based account of how cognitive systems are to be individuated. More than just standing as a counterexample to the historically established

view that demarcates cognitive systems along agential lines, non-agential individuation has important consequences for non-traditional ontologies of cognition, of which dynamicism (van Gelder 1995; 1998; Thelen et al. 2001) is of note.

The agent is generally attributed a mediatory role in accounts of cognition, as it is the receiver of sensory input and the formulator of motor output. Thus, eliminating the agent results in direct interactions between sensory and motor states, such as is exhibited by the state evolution of dynamical systems. In fact, this feature can be expanded into the claim that agentless cognitive systems must be of a dynamical nature. Cognitive systems require that there be a way for sensory input to be transmuted into motor output, and for motor output to be informed by sensory input. In the absence of representations and user systems, the most plausible alternative would be reciprocal causal interdependence between the substrates of processing and effector operations. The resulting system would then be more tightly integrated than its agential counterpart, due to the immediacy of the interactions between its components. Thus, non-agential individuation of cognitive systems gives added theoretical support to the dynamical approach to cognition.



# PART III

## CONSCIOUSNESS

The chapters in the previous section have focused on how octopus cognition is shaped by the physical features of the animal's nervous system. In particular, they jointly demonstrate that octopus cognition is a hybrid of formats and mechanisms that have often been held to be incompatible with each other. In effect, the octopus is presented as an encapsulation of cognitive diversity, a single-organism reflection of the major formats in which biological cognition is realized. As such, either of two explanatory strategies can be adopted when accounting for octopus cognition: piecemeal application of a representational or a dynamical framework to individual cognitive routines, or using a single theory whose explanatory toolkit is fit to handle diverse and dissimilar forms of cognition.

However, there is another contentious domain within the study of the mind for which the octopus carries extensive implications: *consciousness*. Consciousness has been defined in numerous and diverse ways, so it is necessary to specify that the proceeding chapters are concerned with its construal as first-person subjective or qualitative experience, otherwise known as *phenomenal consciousness*. While consciousness-friendly circles of theoretical and empirical approaches to the mind acknowledge that there remains an explanatory gap between subjective experience and its neural substrates, there is widespread consensus that where consciousness appears, its structure is inextricably influenced by that of the nervous system that generates it. This issue in itself has long been a vexed one, and its famous moniker of “the hard problem of consciousness” (Chalmers 1995) is well deserved.

Difficulties aside, philosophical and scientific studies of consciousness have been able to flourish, in large part due to the intuitive appeal of their subject matter. While it had been dismissed at certain points in the past as being epiphenomenal or causally inefficacious, consciousness has been vindicated by empirical research that confirms its



causal role in intelligent behaviour, especially with regards to motor control (Merker 2005; Cole and Paillard 1998; Baars 2005). As such, consciousness has regained substantial recognition as a legitimate element within philosophical, neuroscientific, and psychological approaches to the study of the mind. For these reasons, an investigation into the unique insights the octopus's unusual nervous system provides into the nature of the mind must include some words on consciousness. To address this need, the last two chapters of this thesis are dedicated to exploring what first-person subjective experience would be like in an octopus.

The octopus's vertebrate-like cognitive capacities and the behavioural outcomes associated with them have been regarded as being among the principled reasons to believe that the octopus is conscious (Mather 2008). These types of behaviour call for the participation of various cognitive domains, but as a result of the structure and organization of the octopus nervous system, they do not have the same neural conduits for information transfer as they would have had in vertebrates. The physical features of the octopus nervous system significantly increase the difficulty of carrying out integrative and coordinative neurocognitive functions, which thus may require assistance from another mechanism with similar causal functions. As will be discussed in more detail in Chapter 8, consciousness is one such mechanism (Baars 1983; 2002; 2005; Barron and Klein 2016). Furthermore, the *Cambridge Declaration on Consciousness* of 2012—which summarizes the criteria and desiderata for consciousness attribution to non-human animals—has endorsed neurological bases for ascribing consciousness to the octopus. In particular, these are its possession of the relevant “neuroanatomical, neurochemical, and neurophysiological” (Low 2012) conditions that have been identified as substrates of conscious states.

At this point, a caveat must be issued. Due to the practical and theoretical difficulties of conclusively attributing consciousness to non-human animals, the following chapters will *assume* that the octopus is conscious. A conditional approach will be taken, to reduce the number of theoretical moving parts and to allow the discussions to get off the ground; nevertheless, more detailed justification for attributing consciousness to the octopus will be provided in Section 7.2 of Chapter 7. Thus, the overall explanatory concern of the two chapters constituting this latter part of the thesis revolves around the following theme: *If* the octopus were indeed conscious, what would its consciousness be like? Chapter 7 probes this issue by investigating whether the traditional view that consciousness must be unified applies to the octopus. Chapter 8 brings the discussions constituting this thesis

to a close by exploring whether octopus consciousness plays the same functional roles as its vertebrate counterparts.

## MAKE UP YOUR MIND:

# THE OCTOPUS AND THE UNITY OF CONSCIOUSNESS<sup>1</sup>

Where the existence of consciousness is accepted, it is acknowledged that its configuration is correlated with that of the nervous system generating it. As such, it is unlikely that the sort of subjective experience that would arise from the highly decentralized octopus nervous system would bear much structural resemblance to that of its vertebrate counterparts. In particular, octopus consciousness may not exhibit unity, which has long been assumed to be the normal or default structure of consciousness. This chapter explores whether neurological and behavioural evidence points to octopus consciousness being unified or disunified.

### 6.1 Introduction: Consciousness, the nervous system, and the octopus

The view that consciousness is unified is a long-standing one; indeed, when speaking of consciousness, it is almost always taken for granted that it is unified. This commitment can be expressed via the *unity thesis* (Bayne 2010), the claim that it is only possible to have a single stream of conscious experience at any given point in time. While there are many types and definitions of consciousness, and consequently various ways in which it can be unified, what has been the most frequent object of investigation is the unity of *phenomenal consciousness*. Broadly construed, phenomenal consciousness is what affords a creature “something it is like” to be that creature (Nagel 1974); likewise, a mental state is

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<sup>1</sup> A modified version of this chapter was published online in November 2017 in *Biology and Philosophy*.

phenomenally conscious if it is accompanied by a distinct experiential character. Tim Bayne (2010) enumerates various ways in which conscious states can be unified: by being experienced synchronically or diachronically by the same subject (*subject unity*), being integrated into a single complex experience (*representational unity*), or by there being something it is like to conjunctively experience distinct mental states (*phenomenal unity*). Bayne also presents a useful distinction between the *field* and *stream* metaphors used in discussions on the unity of consciousness: A *conscious field* is the conjunction of all conscious states experienced at a single time, while a *conscious stream* refers to the series of conscious states experienced over the passage of time (Bayne 2010).

The time-honoured commitment to the unity of consciousness comes as no surprise, in large part due to two factors pervasive in cognitive science. First, a sizeable portion of the corpus of consciousness studies is concerned with creatures with integrated and centralized nervous systems—for the most part humans, and later on, certain cognitively complex vertebrates. Second, there is an abundance of physicalist commitments pertaining to the ontology of consciousness, such that it can be presupposed that consciousness is neurally grounded (Bayne 2010). This assumption that consciousness is neurally grounded—which likewise will be accepted here, and termed *neuralization*—is of utmost importance, as it provides a starting point for ontological and epistemological studies of consciousness to get off the ground. Such theoretical underpinnings allow acceptance of empirical evidence that the physical features of a creature’s nervous system influence the structure of its consciousness. This notion can be referred to as the *parallelism thesis*.

A commitment to neuralization entails accepting the parallelism thesis, which holds that the kind of nervous system a creature is equipped with determines the kind of consciousness it has, i.e., the types and complexity of conscious experiences it can undergo. Thus, the type of consciousness we humans have arises as a consequence of the functional and structural properties of our nervous system; our neurophysiology is such that it supports the robust conscious states that we experience. If neuralization is accepted as true, then it is reasonable to suppose that the more features associated with generating consciousness the nervous system of a non-human animal has in common with ours, the stronger the structural resemblance between its consciousness and human consciousness will be. Because human consciousness is typically unified, and has been used as the sole model of subjective experience for a very long time, unity has come to be viewed as a major defining characteristic of consciousness.

These lines of argument are reflected in Bayne's endorsement of the position that *human* consciousness is necessarily unified. Nevertheless, he firmly—and rightly—states that unity should not and cannot be expected to hold for *all* forms of consciousness. While unity may be the default structure of human consciousness, he points out that there are no binding theoretical or empirical reasons to presume that consciousness in other animals in which it is present should be the same. His commitment to neuralization allows him to argue that non-human consciousness does not have to be unified by way of the fact that “some creatures simply won't have the cognitive machinery required to integrate the contents of the mental states in the appropriate manner” (Bayne 2010, 106).

One of the most compelling pieces of evidence for neuralization is the *split-brain syndrome*. First brought to philosophical attention by Thomas Nagel (1971), the split-brain syndrome is often observed in individuals who have undergone brain bisection, a surgical procedure used to prevent the inter-hemispheric spread of epilepsy. While there are variants to the procedure, the basic principle is that fibres in the *corpus callosum*, which connects both hemispheres of the brain, are severed. In humans, many cognitive domains are localized to a single hemisphere, resulting in an asymmetric distribution of neural processing. Severing inter-hemispheric connections, in whole or in part, deprives the brain of conduits through which information is transferred. Interestingly, brain bisection patients exhibit no anomalies in their everyday behavioural and cognitive tasks, yet under experimental conditions the discrepancy between information transfer and first-person reports of conscious experiences is revealed.

The pathology of consciousness characteristic of the split-brain syndrome is demonstrated by the well-known “*key-ring*” test. Here, a compound word such as “key-ring” is presented to the patient so that the visual field of each eye sees only half of the word, i.e., the left eye can only see “key” and the right eye only sees “ring”. Due to the contralateral nature of visual processing, input to the left visual field, i.e., “key”, is processed in the right hemisphere, while input to the right visual field, i.e., “ring”, is processed in the left hemisphere. Because the domain responsible for speech is located in the left hemisphere, the patient verbally reports that all she sees is the word “ring”. However, when instructed to reach for a key with her left hand, she is able to do so, although she is unable to issue verbal reports about the object. Although minor variations have been made to the experiment's setup, the basic findings are that “information presented in the [right visual field] will be unavailable for left-handed grasping behaviour while information presented in the [left visual field] will be unavailable for verbal report” (Bayne 2010, 192).

It thus appears that patients may be able to have two distinct yet simultaneous conscious experiences, one for each side of the body, and in such a way that each side does not appear to be “aware” of the experiences of the other.

In an earlier work on the same subject, Bayne explicitly states that “it is possible that the unity of consciousness might fail in nonhuman animals” (Bayne 2008, 300). Presupposing the parallelism thesis, or the claim that there is correspondence between the structure of an organism’s consciousness and that of its neural architecture, an animal in which a disunified consciousness is most likely to appear would be one with a decentralized nervous system, which precludes complete integration of mental or neural states. An animal that fits this bill perfectly is the octopus. Octopuses are believed to be among non-human animals in which subjective experience is likely to be found, on the basis of their possessing neural substrates associated with consciousness, as well as their repertoire of sophisticated and intelligent behaviour (Mather 2008; Vitti 2013).

The very organization of the octopus nervous system itself calls into question whether it can support a unified consciousness at all (Godfrey-Smith 2013). Notably, unlike the other species to which consciousness has been attributed, the octopus is an invertebrate with a nervous system that is functionally decentralized, a neural organization that entails a distributed cognitive architecture. Furthermore, the extent to which the sensorimotor system of the arms is self-contained, as well as their capacity to retain responsiveness to stimuli even after being amputated, suggests that octopus arms may be capable of experiencing local conscious states. Now, if the brain and the arms can generate local and idiosyncratic conscious fields, the issue arises as to whether subjective experience in an octopus would be unified, given the sparseness of interactions between the components of its nervous system. Yet another highly atypical feature of the octopus nervous system is the lack of central mechanisms for proprioception and somatotopic mapping—both of which contribute vital content to consciousness. This indicates that spatial information about its body is not integrated within a single neuroanatomical structure, but is distributed throughout the nervous system, which in turn raises questions about whether octopus consciousness has a proprioceptive component.

## **6.2 Consciousness attribution**

Although the approach taken presupposes octopus consciousness, grounds for attributing consciousness to a creature in the first place—sophisticated behavioural repertoire or no—

must be presented. One principled reason is that consciousness is believed to contribute to an organism's capacity for adaptive behaviour. It has been argued that consciousness is a mechanism that integrates information from various neural subsystems that do not have direct access to each other, thereby facilitating communication and coordination (Baars 2005; 2002; 1983). The structural idiosyncrasies of these contributing systems have causal influence on the format of their respective outputs, preventing them from having direct access to each other's information. This multiplicity of formats can lead to conflicting or inconsistent information, which when directly transmitted to the motor effectors can wreak havoc on behaviour production.

The integrative nature of consciousness entails that one of the functions of its underlying mechanisms is synthesizing information from various sources before making it available to the motor system, thereby ensuring that the organism's movements are coherent. Furthermore, by integrating the input of diverse subsystems, neural resources that would otherwise have been used to process their individual contributions can be reserved for decision-making operations that pertain to organism-level behaviour control (Merker 2005). The integrative function of consciousness also sets the stage for complex cognitive capacities, such as self-monitoring, control and adjustment of behaviour, decision-making, and adapting to novel or unpredictable situations, as it enables information exchange across a broad range of cognitive domains (Baars 1997). In its highly sophisticated forms, consciousness has also been linked to cognitive capacities involving mental time travel, such as planning and memory, as it allows the subject to construct mental models of actions and their possible consequences (Mandler 2003).

It has been proposed that the evolutionary emergence of consciousness was influenced by the need of sensate organisms capable of self-generated motion to delineate between their bodies and the external world (Merker 2005). In these motile organisms, sensory states can be triggered not only by external stimuli, but also by internally generated causes. Thus, in order to determine whether a behavioural response to such states is warranted, the organism must be capable of distinguishing whether they are internally or externally induced. Because interoceptive information is an important component of consciousness, the organism is thus provided with a means of monitoring its overall physical state. The importance of this monitoring function is highlighted when it comes to motor control, in which the organism requires a reliable mechanism for keeping track of the trajectories, appropriateness, and effectiveness of its actions.

It has been argued that in order for consciousness to perform its integrative and monitoring functions, it must be unified (Baars 1983). Because the neural mechanisms responsible for generating conscious experience work towards coherence, they will inevitably try to smooth out any discrepancies or conflicting input, such as that which can arise from simultaneously experiencing multiple conscious fields. Furthermore, due to the spatiotemporal constraints of human and vertebrate anatomy—which models of consciousness have long been based on—maintaining a single, unified conscious field allows the effectors to be used in a coordinated manner to produce coherent and organized behaviour.

It thus appears that the notion that consciousness must be unified is heavily influenced by the neuroanatomical features of vertebrates. However, the octopus, with its decentralized cognitive system and arms with identical sensorimotor capacities, does not face the same physical constraints that vertebrates do. Consequently, the question arises as to whether attributing consciousness to the octopus also entails committing to the unity thesis.

### **6.3 Multiple conscious fields?**

The extensive functional self-sufficiency of octopus arms and the sparse connections between the central and peripheral components of the nervous system indicate that sensorimotor information from the arms is processed locally before being sent to the brain (Hochner 2004). Taken in light of the neuralization thesis, these features motivate the notion that octopus arms may support local conscious fields that are independent of the main field, whose substrates are found in the brain. If so, then the sensorimotor responses of an amputated octopus arm to stimulation would be accompanied by corresponding subjective experience, so that—in Nagel’s (1974) words—there would be something it is like to be an octopus arm.

It is suggested by empirical findings (e.g., Rowell 1963; Sumbre et al. 2001) that an isolated octopus arm supports a field of *primary consciousness*, in which subjective experience is parsed as sensory awareness. For primary consciousness to be attributed to an organism or a system, all that is called for is that it be capable of “direct awareness of the world without further reflection upon that awareness” (Barron and Klein 2016, 4901). The substrates of primary consciousness must thus be able to register sensorimotor information in such a way that they give rise to “an integrated simulation of the animal’s



own mobile body within the environment” (Barron and Klein 2016, 4901). That the octopus arm contains and can activate the motor patterns of stereotypic movements, and retains its responsiveness to stimulation post-amputation suggest that such an internal model may be present in it.

In vertebrates, attributing distinct conscious fields to components of the nervous system that have sensorimotor processing and control functions is an ill-advised move. While such neural structures can carry out their operations with a certain degree of autonomy, they do not have the same extent of influence over behaviour production as the octopus arm does. The centralization of vertebrate nervous systems entails that while some sensorimotor operations are distributed to peripheral components, the bulk remains concentrated within the brain. As the result of its unique evolutionary development, the reverse is true of the octopus: the arm nervous system has the main responsibilities when it comes to fine-grained motor control and processing sensory—tactile, mechanical, and chemical—information. Consequently, the organization of the octopus nervous system is such that its central and peripheral components are functionally specialized, with the brain and the *axial nerve cords*—the neuronal tracts found within each arm that connect it to the brain and integrate local sensorimotor information—alike being high-level processing and control centres (Richter et al. 2015). Thus, it is the extent of functional self-sufficiency of the octopus arm that renders attributing consciousness to a peripheral neuroanatomical structure a plausible move, where it is not in vertebrates.

Interestingly, despite the fact that the arms are not somatotopically represented in the motor centres of the brain, the octopus appears able to alternate between central and peripheral motor control (Gutnick et al. 2011; Godfrey-Smith 2013). The observation—which was quoted earlier in the thesis—that while octopus arms are “curiously divorced” from the brain, “octopuses can exert a significant degree of central control over their arms when they need to” (Godfrey-Smith 2013, 8) is worth reiterating. In an important study conducted to determine whether octopuses are “capable of guiding a single arm in a complex movement to a location”, which entails integrating “peripheral arm location information with visual input to control goal-directed complex movements” (Gutnick et al. 2011, 460), subjects were tasked with retrieving food from a maze. The test conditions were such that they unequivocally demonstrated that the octopuses could use only visual input, and not chemical or tactile information, to successfully complete the task. The maze was designed to ensure that, while the octopuses could use stereotypic movements such as extension and probing, reaching the reward required their arms to enter into positions not

typically used under natural conditions. The task itself thus demanded a degree of precision that could be brought about only through visual guidance, which indicates central motor control: *feed-forward* control, or the use of pre-planned motor commands, was ruled out as unlikely, due to the “‘crawling and probing’ nature of the search movements” (Gutnick et al. 2011, 462).

The integration of visual information with motor commands was interpreted as indicative of central control over the arm as it executed the retrieval task. These findings suggest that the brain and the arm nervous system are capable of exchanging and consolidating information about the position and location of the arm, which is significant given “the lack of somatotopic representation of the body in the higher motor centres as well as the inability to elicit single-arm responses in stimulation experiments” (Gutnick et al. 2011, 462). Such precision in motor control is not unheard of in the octopus: much of its behavioural repertoire is comprised of actions that demand fine movements, such as stacking and carrying around halved coconut shells to use as portable shelters (Finn et al. 2009), and using their arm tips to cleanly pick the flesh of crabs apart from their shells (Boyle 1986; Mather 2008). These factors make the octopus a puzzling, almost counter-intuitive, case in motor control: it is able to execute complex movements that call for precise and detailed control, without the benefit of proprioceptive information and somatotopic representation in the motor centres of the brain.

Gutnick et al.’s findings are surprising, given the way in which the octopus nervous system is functionally organized. How does integration of visual and proprioceptive information come about, if neuroanatomical evidence indicates that the latter does not reach the brain? Or perhaps they are not integrated at all: if the brain and the axial nerve cords are high-level control centres, then perhaps they separately process central and peripheral input, respectively. What may be the case is that the motor control scheme underlying the retrieval task—and other movements that require deviation from familiar motor patterns—is the outcome of the *coordinated* operations of brain-based and arm-based control centres, rather than centrally generated motor commands that subsume peripherally sourced information.

Presupposing the neuralization and parallelism theses, such a motor control scheme gives credence to the possibility of distinct and separate brain-based and arm-based conscious fields in the octopus. If the structure of consciousness divides along the same lines as the functional organization of the nervous system, it is likely that octopus consciousness is constituted by local fields that are experienced simultaneously, but are not

integrated. Such non-integration would be due to the structural and functional dissimilarities between the brain and the arm nervous system, which entails the strict localization of neural routines.

Consequently, the contents of the distinct conscious fields would vary according to the sensory modalities their substrates support and traffic in. Brain-based consciousness would subsume visual experiences and presumably global sensations of position and motion, while chemotactile and proprioceptive information about the state of the arms would be encompassed within the arm-based field (or fields). There may be some overlap of contents between central and peripheral conscious fields, but only to the extent that they can be supported by the respective substrates of either field.

#### **6.4 The octopus and the unity thesis**

So far I have presented arguments for believing that octopus consciousness would be disunified. If correct, they would hoist the octopus as a biological counterexample to the unity thesis, which holds that wherever consciousness is instantiated, it is unified. Presupposing neuralization, the structural and functional integration of the brain makes it the most plausible location for the substrates of consciousness. Thus, it is likely that the qualitative experiences accompanying neural processes excluded from or unable to reach the brain do not enter into the brain-based conscious field. However, this does not entail that such neural operations are entirely non-conscious: They may still be consciously experienced, albeit not as part of the main conscious field, which is localized in the brain. Bayne (2010) argues that this is not possible in humans, due to the neurophysiological and anatomical limitations of our nervous system. However, he does not extend this claim to other creatures; indeed, both the nervous system and body plan of the octopus are such that they could plausibly support multiple, non-unified conscious fields. To provide a broader context within which to nest the issue at hand, I will present a number of alternatives or opponents to the unity thesis and discuss how they contribute to the investigation.

##### *6.4.1 Nagel: Uncountable minds*

In his discussion of the split-brain syndrome, Nagel (1971) argues that such subjects do not have a countable number of minds. He points out that their capacity to experience more than a single phenomenal field at a time suggests that they do not have just one mind, yet the normalcy of their everyday behaviour precludes a clean and unequivocal division into

two streams of consciousness. Furthermore, the usual epistemic ports of call are not of much help here: neither behaviour nor neuroanatomy can decisively settle the question of how many minds split-brain patients have. The apparently incomplete integration of conscious experiences taken together with sufficiently unimpaired behaviour they exhibit thus undermines the claim that conscious states have to be unified in order to produce coherent behaviour. In subjects with intact brains, conscious experience may be completely integrated, but it follows from Nagel's account that consciousness does not have to be unified in order for it to be an effective control system. Thus, Nagel's view entails that unity is not a necessary condition for consciousness to play its functional roles, which pertain to ensuring behavioural coherence. Nagel even goes as far as to suggest that our concept of unity may run counter to the way the physiological operations responsible for controlling our behaviour actually work. He writes that in maintaining that normal consciousness is unified, we may be "subtly ignoring the possibility that our own unity may be nothing absolute, but merely another case of integration, more or less effective, in the control system of a complex organism" (Nagel 1971, 410).

#### 6.4.2 O'Brien and Opie: *Multi-track polyphony*

An outright denial that consciousness is unified comes from Gerard O'Brien and Jon Opie (1998). They introduce a *multi-track polyphonic model* that construes the field of phenomenal experience as an amalgam of distinct cross-modal contents experienced simultaneously. Based on an analogy to music, the polyphonic model holds that multiple conscious contents are experienced simultaneously, i.e., as part of a single experience. They caution that this view is easily misread as meaning that input from different modalities must be transmitted to mechanisms that will bind them into a single experience, which is then broadcast to cognitive systems. They clarify that polyphony is correctly understood as the mingling of voices to produce a single sound wave, in which case a single experience arises from the contribution of distinct components. While the end result is a coherent and connected product, the components do not lose their independent qualitative properties, so it is still possible to identify and distinguish between the parts.

In endorsing multi-track polyphony, O'Brien and Opie retain the basic principle behind polyphony—i.e., simultaneous cross-modal experiences—but do not accept that they are unified. To be more specific, they do not endorse the notion that cross-modal experiences have to undergo *binding*, or fusion into a single multi-faceted mental state; instead, the feeling that they are all part of a single experience arises from the fact that they

are undergone simultaneously. Thus, they claim that consciousness is not unified, but *manifold* because it is a composite of numerous distinct and discrete experiences, and *distributed* because the mechanisms that generate these experiences are spread throughout the brain (O'Brien and Opie 1998, 393).

#### 6.4.3 *Two-streams and partial unity*

Although he argues that the unity of consciousness holds even in split-brain patients, Bayne notes that there are two models of consciousness commonly used to account for the purported disunity experienced by split-brain patients (Bayne 2008; 2010). First is the *two-streams model*, on which the subject's phenomenal states can be divided into two sets, where the states within one set are all phenomenally unified with each other, but there is no unity of states across sets. The other is the *partial unity model*, which holds that some experiences are unified with each other but not with others, so that an experience *e3* would be unified with *e1* and *e2*, but *e1* and *e2* would not be unified with each other.

Both models call the unity thesis into question in related but slightly different ways. The two-streams model is an upfront denial of the main claim of the unity thesis, that humans can have only one stream of consciousness at any given instance. With regards to the functional role of consciousness, the two-streams model demonstrates that it is possible to generate coherent behaviour even though the subject has multiple fields of consciousness. That is to say, it runs contrary to empirical claims that the mechanisms of conscious experience have to remediate conflicting, inconsistent, or simply non-complementary information in order for it to be useable in behaviour production (e.g. Baars 1983).

The partial unity model can be read as a more nuanced view of the two-streams model; it does not connote two self-sufficient conscious streams, but suggests that there is a principal conscious stream and straggler conscious states. While the principal stream would be responsible for the bulk of behaviour production, the "loose" states are not epiphenomenal. They would be involved in certain sub-tasks of behaviour, but would not be experienced as part of the principal stream. A messier interpretation is also possible, such that instead of a principal conscious stream and individual unified ones, some loose conscious states would be unified with some others, producing sub-unified states that could even overlap with each other. Much like Nagel's view, this would be highly problematic when it comes to determining how many conscious streams are present. Thus, the partial unity model differs from the two-streams model in its disagreement with the unity thesis in

that it does not allow consciousness to be divided along clean lines.

#### 6.4.4 *Assessing the views*

Rather than an outright debunking of the unity thesis, I treat Nagel's view as taking it on modal grounds. Nagel accepts the correlation between neural and mental structures, yet points out that the resulting dissimilar structures of consciousness still produce coherent behaviour, thereby blocking the way of any functional claims to necessity the unity thesis may make. Thus, the conclusions arising from Nagel's view establish a firm foundation for arguments that the behaviour of creatures with neural architectures that make the endowment with a unified consciousness unlikely or uncertain should not be dismissed as non-cognitive.

O'Brien and Opie cite temporal simultaneity as being responsible for why we feel that conscious states occurring at the same time are a single, unified state. Due to their dismissal of binding, their account sets a theoretical stage for the possibility that the substrates of consciousness can be found in various parts of the body. While all they claim is that the mechanisms of consciousness are distributed throughout the brain, the same principle is applicable to a creature such as the octopus whose nervous system is distributed throughout its body in such a way that its peripheral components are complex enough to plausibly support primary conscious experience. The notion of binding implies that conscious experiences must be transmitted to a mechanism or mechanisms that integrate them with each other. Such mechanisms must thus have access to information provided by the distinct substrates of individual conscious states, which undoubtedly include proprioception.

In contrast, the multi-track polyphonic model makes it possible (at least theoretically) that conscious states can be experienced as such wherever they are physically localized. Now, there is reason to think that an octopus arm on its own is capable of at least primary consciousness, due to its ability to respond to stimulation and exhibit pain behaviour even when isolated from the brain. However, the octopus's neuroanatomy suggests that detailed interoceptive information about the arms does not reach the brain. If conscious states can be experienced locally and without the involvement of a binding or integrative mechanism, then it is possible to arrive at a positive answer to the question of whether an octopus can feel its arms even without central somatotopy and proprioception, as well as a plausible explanation of how this takes place.

The two-streams and partial unity models come into close proximity of what an

octopus's consciousness might be like given the organization of its nervous system. The interbrachial commissure is a neural structure that interconnects the octopus's eight arms, and allows them to communicate with each other at the peripheral level. Thus, it may be the case that the interbrachial commissure functions as an integration mechanism that permits the arm nervous system as a whole to give rise to a consciousness of its own. This *peripheral consciousness* would not be as complex as the one whose substrates are in the brain, which can be termed the *central consciousness*, being limited to sensorimotor experiences from the individual arms. Nevertheless, it would be distinct from the central consciousness, thus endowing the octopus with two conscious fields.

The partial unity model, on the other hand, can be applied if we were to do away with the proffered integrative role of the interbrachial commissure. Instead, the unified peripheral consciousness will be replaced with individual conscious streams for each arm, i.e., *arm consciousness*. Like peripheral consciousness, arm consciousness would consist of local sensorimotor experiences, but would not be unified with the streams of other arms. There are empirical bases to support arm consciousness, the most notable of which is the capacity of amputated arms to behave “normally” when stimulated (Rowell 1963). While they differ slightly from each other, the two-streams and partial unity models both offer theoretical precedents that are helpful to understanding what octopus consciousness may be like.

## **6.5 Octopus consciousness: Unified or disunified?**

The morphological arrangement and the extent of functional autonomy of the components of the octopus nervous system raise the question of whether it can support unified conscious experience (Godfrey-Smith 2013). Furthermore, the position that favours disunity is motivated by the octopus's lack of central somatotopic representation, proprioception, and the extent to which sensorimotor processing and control responsibilities are offloaded to the periphery. Indeed, the octopus is an exemplar of an animal in which “the unity of consciousness might fail” (Bayne 2008, 300), thereby demonstrating that consciousness is not necessarily unified.

Furthermore, the octopus directly challenges the functional claim made by the unity thesis, i.e., that the only structure of consciousness that can generate coherent behaviour is a unified one. Indeed, the evolutionary success of the octopus bears itself out as evidence that an organism whose consciousness is disunified can nevertheless have psychological

and behavioural capacities on a par with those associated with organisms with a unified consciousness. This in turn casts long shadows on discussions on the role of consciousness with regards to intelligence and behaviour: rejecting the notion that intelligent behaviour presupposes a unified consciousness revokes the privileged status of models of cognition that put a premium of centralized nervous systems, which dominate cognitive science and which the unity thesis has implicit commitments to.

The structure of consciousness of humans with *proprioceptive deafferentation*, or the pathological deprivation of sensation, bears resemblance to what octopus consciousness can be expected to be like. Somatosensory information, especially proprioception, is crucial to internal awareness of one's own body, which in turn enables fine-grained control of behaviour. In other words, the interoceptive information that enters into the field of consciousness is what makes it possible for consciousness to carry out its functional roles, especially those that pertain to self-monitoring and behaviour control. However, there exist cases wherein precise behaviour can be produced without the subject being interoceptively aware of what is going on. A well-known clinical example is that of Ian Waterman, who lost all proprioceptive sensation from the neck down (Cole and Paillard 1998). Although deprived of internal awareness of his body, Waterman is able to get on with his day-to-day activities by visually guiding his movements. Interestingly, although for the most part he has to use visual monitoring to perform bodily actions, he has retained his ability to gesture naturally. Waterman himself reports that controlling his movements takes a lot of conscious mental effort, and demands his full attention.

A similar case is autobiographically reported by István Aranyosi (2013), who sustained temporary damage to his peripheral nervous system as a result of chemotherapy. Consequently, proprioceptive input and motor control of his limbs were compromised. He describes a number of compensatory measures he took to guide his movements, such as using vision and coarse-grained proprioception from the more central parts of his body, as well as mechanical constraints imposed by the external environment and his very morphological structure. In both Waterman's and Aranyosi's cases, consciousness functions as an "alternative" mechanism that takes over motor control when the normal neural pathways have been compromised.

Cases such as these suggest that while the motor centres of the brain receive proprioceptive information from the relevant body parts, it fails to enter into the subject's conscious experience. In such cases of proprioceptive deafferentation, it may be that the unity of the person's consciousness is not fractured into multiple streams or fields. Instead,



it appears that such consciousness is not *comprehensive*, or inclusive of all the states associated with conscious interoceptive monitoring and motor control. That is, the brain receives, processes, and utilizes information from deafferented bodily sources, but this information does not enter into conscious experience. (It must be noted that *comprehensive unity* differs from partial unity in that it does not claim that the states that do not enter into the main phenomenal field are nevertheless conscious.) Likewise, the octopus brain would receive and use information from its arms, but doubts may be raised as to whether such information is of the conscious sort. Assuming that the mechanisms responsible for generating consciousness are found only in the brain, brain-centred octopus consciousness can be expected to exclude interoceptive experience of the arms. Thus, if consciousness were generated only by brain-based mechanisms, an octopus would have a single conscious field, but it would not be a comprehensive one.

However, there is a crucial difference between the octopus and deafferented humans. Due to the structure and organization of the human nervous system, it would make little sense to ask whether there is something it is like to be the foot of a deafferented human. The neural equipment of the foot is insufficient to support, much less generate, conscious states when taken in isolation from the brain. By contrast, an octopus's arm is self-sufficient in terms of its sensorimotor functions. As discussed earlier, such a neural organization leads to principled and plausible reasons to believe that an octopus arm may be able to support conscious experience. Yet, this remains an open question, as it may well be the case that the responses to stimulation exhibited by isolated or amputated octopus arms are unaccompanied by phenomenal character. What, then, are the consequences of the presence or absence of arm consciousness for what it is like to be an octopus? Each option will now be examined in its turn.

If the brain and the arm network give rise to distinct streams of consciousness that are independent of each other, the lack of proprioceptive information transfer implies that the octopus would simultaneously maintain multiple, disunified conscious fields. At any given point in time, the octopus would experience any conscious central and peripheral states occurring then, but they would not be bound into a single multi-modal experience. Instead, these states would be experienced at the same time, giving them the feel of being part a single conscious field, but they are not integrated with each other. Thus, if the brain and the arm network were to be physically separated from each other, qualitative experience in either component would consist solely of the conscious states whose substrates are localized it in. This decomposition runs along the lines of what O'Brien and

Opie (1998) propose. In this case, conscious unity fails altogether, thereby rendering the octopus as a counterexample to the claim that consciousness has to be unified to produce coherent, intelligent behaviour.

But what would the outcome be if the arms, on their own, do not generate consciousness at all? Any phenomenal experiences the octopus would have of its arms would have to be centrally generated—but without somatotopic representation and proprioception, it is difficult to see how this is even possible. Thus, while the octopus would have a single, central conscious stream, it would not subsume experiences of the motor states of its arms, and hence would not be comprehensive. In this case, control over arm movements would be realized through the use of non-conscious local and dynamical mechanisms, thus demonstrating that motor control can take place even though proprioceptive information about the relevant effectors does not enter into conscious experience.

In summary, the nervous system of the octopus is such that it may neither generate nor support a unified consciousness. Furthermore, the neurophysiology of the octopus is an actual organic instantiation of a system that does not require full, comprehensive conscious access to internal control mechanisms to produce behaviour. The following lessons can thus be learned from the octopus. First, that it is an actual evolved example of an animal in which the unified model of consciousness is not likely to hold; and second, that it is a counterexample to the claim that a unified consciousness is prerequisite to intelligent behaviour.

## **STRONG-ARM TACTICS:**

# **THE OCTOPUS AND THE ADAPTIVE FUNCTIONS OF CONSCIOUSNESS**

The previous chapter examined the structures of consciousness that the octopus nervous system can possibly and plausibly give rise to. In line with its decentralized neural and cognitive architecture, it was argued that it is unlikely for consciousness in the octopus to exhibit unity, a feature that has long been held to be the default or normal characteristic of subjective experience. This chapter builds on the foundations set by the last one, and examines whether consciousness in the octopus plays the functional or causal roles attributed to consciousness in general.

### **7.1 Introduction: Finding a place for consciousness**

For many decades, any talk of consciousness was excluded from empirical and theoretical approaches alike to the study of the mind. The inability to determine exactly how consciousness arises has led to difficulties in quantifying it, and thus hesitation to accept it as a genuine causal phenomenon or legitimate explanatory tool. While the existence of consciousness has largely been an intuitive notion, incorporating it into mechanistic accounts of the mind—which are favoured due to their ontological and epistemological parsimony—has often been considered imprudent. Observing the physical states undergone by an organism’s nervous system as it performs certain actions is possible, and thus causal correlations between neural activity and behaviour can be made with relative ease. Conscious states, however, are much more elusive: although neural activity that

accompanies various conscious experiences can be identified, doing so does not answer the question of *how* the latter causally originate from the former, or how consciousness arises.

As the grounding of consciousness in the nervous system is a fundamental starting point in a third-person-observable approach to consciousness, the inability to establish it as a quantifiable element is a deterrent from exploring aspects of it that may be causally relevant. The reluctance to incorporate consciousness into theories of the mind stems from the worry that there is too much uncertainty surrounding it to support the weight of mental and behavioural phenomena being attributed to it. Over time, the accumulation of difficulties in observing and quantifying consciousness led to its being dismissed altogether as an unreliable, merely folk-psychological notion, with no causal participation in neural and psychological processes whatsoever. Thus, much of modern neuroscience has considered appeals to consciousness as empirically and theoretically unacceptable (Mandler 2003).

In addition to empirical suspicion, consciousness has met with its fair share of hostile philosophical attitudes. Where its existence was not denied outright (e.g., by *eliminative materialists*, of whom Patricia and Paul Churchland are notable), it was considered causally inefficacious (by *epiphenomenalists*, such as the Behaviourists). In-between positions that recognized the existence of subjective or qualitative experience were likewise hesitant to construe consciousness as ontologically substantive, and usually sought to establish it as parasitic on neural states (e.g., *reductive materialism* in the hands of U. T. Place and J. J. C. Smart). Where the intuitive appeal and capacity of consciousness to support coherent explanations of behaviour were acknowledged, it was nevertheless dismissed as a crude and inchoate option that was used only due to the unavailability of more accurate and dependable explanatory tools (Dennett 1987).

The empirical and theoretical intractability of the issue of how subjective first-person experience arises from a third-person observable neural base is captured succinctly by Chalmers (1995) when he refers to it as “the hard problem of consciousness.” However—and almost paradoxically—such a move is a prudent one that has allowed consciousness to be revisited as a plausible cognitive mechanism, and hence a viable and robust explanatory tool. On one hand, consciousness is too intuitive and ubiquitous a phenomenon for its existence to be denied; on the other hand, it is notoriously elusive to quantification and resistant to direct observation. Acknowledging that its causal grounding in the nervous system is a veritable hard problem prevents having to throw the conscious baby out with the theoretical and empirical bathwater. Signposting this explanatory gap has

made it possible for research to be carried out on the functional roles played by consciousness and its contributions to cognition. These endeavours have yielded interesting and compelling results, such as the finding that consciousness can serve as a mechanism for motor control in cases where the usual pathways are impaired. As such, a number of functional roles that contribute to an organism's biological success by enhancing its capacities for adaptive behaviour have been attributed to consciousness. These adaptive functions of consciousness usually pertain to motor control and self-monitoring.

## **7.2 Accepting the causal value of consciousness**

Among the first contemporary theories of the mind to explicitly posit consciousness as an explanatory mechanism is the influential *Global Workspace Theory*, which was first proposed by Bernard Baars (1983) and has seen further developments since. A key player in neuroscientific literature, Global Workspace Theory views information processing as distributed throughout the nervous system, which is comprised of specialized subsystems that are functionally autonomous up to a certain point. This information is then transmitted to a central processor, i.e., the eponymous *global workspace* or *global data base*. Once in the global workspace, information can be accessed by any subsystem within the nervous system, to be put to use according to the operations it is responsible for.

Consciousness is thereby posited as an agent that is able to handle diverse formats of information. As such, it enables communication and coordination between the various elements of the nervous system, whose structural and functional idiosyncrasies often prevent direct access to each other's output (Baars 1983; 2005). The role of consciousness is compared to a spotlight on a stage, i.e., the *theatre metaphor*, which highlights or draws attention to certain aspects of information that are of particular or critical importance to generating intelligent behaviour. By doing so, consciousness functions as a signal booster that ensures that all the components of the nervous system receive this information and can respond to it appropriately. By functioning as a nervous system-wide information exchange, consciousness thus facilitates the emergence of complex cognitive routines that call for the participation of various cognitive domains.

It has also been proposed that consciousness helps to ensure that complex behaviour is carried out coherently (Merker 2005). Complex behaviour calls for multi-modal sensory information, and the coordinated movements of distinct effectors. In organisms in which sensorimotor operations are considerably offloaded to the periphery, localized processing

and control is carried out in response to specific and limited aspects of information. Such compartmentalization can lead to potentially conflicting input to the nervous system and consequently fragmented motor output, unless the influx of information is subjected to *remediating* operations that synthesize and stabilize it before it is transmitted to the motor system (Baars 1983).

Furthermore, when combined with an advanced memory capacity, consciousness can enable an organism to carry out novel cognitive tasks offline (Dehaene and Naccache 2001). Conscious retrieval of stored information allows the organism to construct mental models of its actions in light of certain environmental conditions, and to anticipate various outcomes that could arise from them. By releasing the organism from dependence on occurrent stimulation, consciousness can equip the organism with the related capacities for mental time travel and reflection (in the sense of being able to mentally evaluate the consequences of its actions).

The previous chapter introduced Bjorn Merker's (2005) influential theory of the evolutionary significance of consciousness, which holds that consciousness enables the organism to distinguish between sensorimotor signals that are generated by self-directed motion—*reafferent states*—and those that are activated by external stimulation—*exafferent states*. This demarcation task, known as the *reafference problem*, is vital to motor control and adaptive behaviour, as it is the point of reference for determining whether a reaction or response to the cause of the sensorimotor signals is appropriate. The reafference problem is compounded in organisms with sophisticated sensorimotor systems and effectors, due to the complexity of the input that they receive and process. It is further exacerbated by movement, which gives rise to additional sensory input that alters occurrent sensory states.

Sensory systems can be categorized as exteroceptive or interoceptive, depending on whether they respond to stimuli that are external or internal to the organism, respectively. Vision and hearing are among the most fundamental—and best studied—exteroceptive senses, while proprioception and kinaesthesia (which monitor the position and movement of the body, respectively) are key interoceptive ones. These sensory systems collectively function as an egocentric model of the world, which provides the organism with information about environmental conditions from a first-person, situated perspective, on the basis of which it produces adaptive behavioural output. Consequently, the motor system must have access to exteroceptive and interoceptive sensory input alike—which usually

entails exorbitant neural requirements due to the need for mechanisms that can process a diversity of information (Dunbar 2007).

What Merker (2005) proposes is that consciousness lowers the neural cost of sensory processing, due to the integrative and remediating functions of the mechanisms responsible for generating it. Consciousness acts as a filter that ensures that the sensory information received by the motor system is a “synthetic, stabilized, and coherent neural simulation of [its] body in relation to its surrounding space” (Merker 2005, 95). As such, there is no need for resources within the motor system to be allocated for lower-level sensory processing and remediating operations, leaving more room for higher-level functions such as coordination and motor planning. Furthermore, the remediating function of consciousness makes it possible to narrow down where it is generated to somewhere between the integration of sensory input and the formulation of motor commands (Haggard et al. 2002).

Consciousness also serves as a signal to the organism that it may be in a state of physiological instability, which may be potentially deleterious to it. Merker points out that many non-sensorimotor bodily processes, such as heartbeat or digestion, are not usually accompanied by conscious experience. However, when their normal functioning is disrupted or impaired, they often arise into conscious awareness (usually in the form of pain or discomfort), prompting the organism to undertake corrective or compensatory measures to regain its physiological stability. In cases such as these, consciousness enables the organism to monitor its internal condition.

Interestingly and importantly, there is significant overlap between the neural architectures associated with sophisticated cognition and those from which consciousness can plausibly arise; it is believed that consciousness-generating mechanisms may be parasitic upon neural resources primarily dedicated to cognitive operations (Mandler 2003; Barron and Klein 2016). It therefore comes as little surprise that the non-human species—e.g., the great apes, dolphins, birds, and octopuses—that have been discovered to be the most cognitively complex are the very same ones that are strong candidates for consciousness. In particular, considerable centralization of the nervous system is typically deemed to be a necessary—but by no means sufficient—condition for consciousness to arise (Barron and Klein 2016). Thus, if consciousness piggybacks on complex cognitive routines, then the benefits for the latter that are brought about by having the various components of the nervous system in close proximity to each other (i.e., less travel time for

neuroelectric signals or neurotransmitters, and a reduced need for signal-boosting mechanisms) also contribute towards the former.

In a nutshell, consciousness is believed to be a neuro-psychological mechanism that scaffolds or supplements complex cognition. As such, it contributes to the organism's biological success by affording it with an egocentric means to monitor both the environment and its overall physical state in light of environmental conditions, thereby enhancing its capacities for adaptive behaviour. The unique contribution of consciousness is that it enables the organism to track the reciprocal effects of its situatedness within the world, i.e., how it is affected by its environment and how its behaviour in turn affects the environment.

While the functions and causal roles of consciousness increase as it becomes more sophisticated, awareness of oneself as an entity distinct from the environment is the most fundamental biological benefit of subjective experience. In particular, consciousness makes it possible for the organism to 1) keep track of the state of its body in light of the internally and externally generated changes it undergoes and 2) update its behavioural or motor output in light of these changes. Such a capacity, which will be referred to as the *self-monitoring function* of consciousness, has been convincingly argued to be in place in the various clades that are accepted as endowed with subjective experience (Merker 2005; Barron and Klein 2016). Common behavioural evidence for self-monitoring includes mirror self-recognition and observational learning; in the octopus, the cryptic technique of rearranging the body outline and locomotion patterns to mimic those of another species is another example.

Nevertheless, the octopus stands out as a creature in which the self-monitoring function attributed to consciousness appears to have a tenuous hold. That is to say, conscious self-monitoring may not play as vital a role to adaptive behaviour in the octopus as it does in its vertebrate counterparts. To begin with, the functional organization of the octopus nervous system evolved as an efficient alternative to a centralized neural architecture, whose biological costs would have proven exorbitant for the octopus (Hochner 2013; Zullo et al. 2009; Sumbre et al. 2001). The consequence of such an organization is that ensuring the appropriateness of the motor trajectories along which the arms travel is only minimally dependent on central control, but is carried out mainly in the periphery through the use of local feedback loops and muscular activity.

If low-level, dynamical operations are almost entirely responsible for monitoring arm movements—i.e., keeping track of their spatial coordinates and updating the position of the arm accordingly—then ascribing such a function to consciousness proves to be



unparsimonious and redundant. Thus, while the octopus nervous system may be capable of generating conscious experience, the causal role played by consciousness within the octopus's cognitive economy may not include the monitoring and motor updating functions attributed to it. In other words, octopus consciousness may be a counter-example to the claim that the most vital and fundamental contribution of subjective experience to an organism's biological success is that it is a self-monitoring mechanism whose reliability is unprecedented. The present chapter explores this possibility, by examining a number of cognitive processes which are normally held to necessitate subjective experience, yet may be realized in the octopus without the causal participation of consciousness.

### 7.3 The self-monitoring function of consciousness

Self-monitoring is not a single function of consciousness, but a cluster of conscious cognitive routines concerned with interoceptively registering the state of the organism's body. These operations, which are often critical to motor control, do not all have the same level of biological fundamentality: some of the complex ones may have evolved out of simpler ones, while the emergence of others may have been scaffolded by concomitant cognitive developments.

Following Merker's view, the fundamental functional role of consciousness is to enable an organism to establish somatic boundaries, i.e., to allow it to demarcate itself from the external world. This entails the capacity to distinguish between sensory states that are internal to the organism and those that are external to it. It also allows the organism to distinguish between its movements that are self-generated, and those that arise as the result of external physical forces being applied to it. This basic monitoring capacity can be referred to as *somatic awareness*.

A more complex form of somatic awareness is *self-recognition*, which implies at least a rudimentary sense of agency. Self-recognition, in turn, can be either *exteroceptive* or *interoceptive*. *Exteroceptive self-recognition*, of which mirror self-recognition is a notable example, is a highly sophisticated capacity in which the organism identifies its own body based on externally-sourced input, usually of the visual sort. It involves experiencing one's body as an external perceptual object, and not through immediate and direct proprioceptive awareness. In contrast, *proprioceptive self-recognition*—which will be the focus of this chapter—is a more basic capacity wherein the organism has immediate interoceptive awareness of its own body. Proprioceptive self-recognition can be further

categorized as either *anatomical* or *functional*. The anatomical type refers to proprioceptive awareness of one's own body parts and their boundaries. Its functional counterpart refers to the complementary abilities to correctly identify first-person perceptual states as being generated within one's own body, and to recognize one's body as the source of such states.

A third function of consciousness, which presupposes somatic awareness and self-recognition (either or both forms, depending on the cognitive sophistication of the organism in question), is *behaviour updating or correction*. This function is especially helpful when the organism is faced with a novel task, wherein it is forced to try out novel behavioural responses or motor patterns. In such cases, the unfamiliarity with how to bring about a desired outcome calls for constant monitoring to ensure that the behaviour or action being executed is appropriate, especially with regard to the correctness of motor trajectories. Much of the motor control aspects of behaviour are unconscious or stereotypic, or both, often leading to perseverating in inappropriate actions (e.g., the A-not-B error, which was discussed in Chapter 3), and hence failure to successfully complete the task at hand. Departing from familiar motor patterns requires the underlying sensorimotor operations to be especially receptive to real-time feedback generated as the movement is executed. Furthermore, novel tasks frequently call for new or untested motor patterns, whose success requires both the movement of the effector and its effects on the environment to be closely monitored and adjusted as it unfolds. While unconscious corrective motor operations sometimes suffice to keep the action on track, there are cases wherein the complexity of the movement demands a more reflective monitoring mechanism, such as that provided by conscious motor control. Often, these are complicated movements that require significant deviations from the natural posture of the body or the effectors.

In sum, the self-monitoring function of consciousness—via the cognitive capacities it subsumes—underpins the possibility of developing a *sense of self*, or the rudimentary awareness an organism has of its own physical boundaries that separate it from the external world, and of itself as the agent of its actions. Nevertheless, there are myriad unconscious processes that indispensably contribute to establishing the sense of self as so defined—and without which it cannot arise. However, the lack of direct communication and the frequent conflict of information between them would prove detrimental to the production of coherent behaviour, so their input must be synthesized before it is incorporated into motor commands. While consciousness does not have the sole responsibility for these integrative or remediating operations, it makes a unique contribution to them by affording the organism with a capacity for reflection, or first-person awareness of its own body and its effects on

the external world. This conscious self-monitoring, which can be referred to as the *reflective function of consciousness*, thus enables the organism to track the appropriateness of its behaviour, particularly with regards to identifying the aspects of its motor output that need adjustment and determining how they can be rectified.

#### **7.4 The self-monitoring function of consciousness in the octopus**

The decentralized nervous system of the octopus radically differs from those of other candidates for consciousness. While the octopus nervous system successfully gives rise to many of the same sophisticated cognitive capacities as those observed in vertebrates, it is unlikely to generate conscious experience with a structure that resembles those of vertebrates. Thus, if consciousness in the octopus departs from familiar structures, does it also depart from the functional roles attributed to consciousness in general? In particular, does it have as vital a role in self-monitoring and behaviour regulation in the octopus as it does in its vertebrate instantiations?

Due to the anatomical and motor hyper-redundancy (wherein every arm has identical anatomical features and motor capacities), extreme flexibility, and lack of proprioceptive guideposts and somatotopic representation entailed by the soft body plan of the octopus, precise motor control is extremely challenging—yet is of the utmost importance. As has been discussed in a number of earlier places, octopuses must be able to select which arms to use to perform a task, activating appropriate ones while suppressing others whose participation would be redundant or cumbersome. Needless to say, they must also ensure that their arms travel along the correct trajectories when executing a movement.

Such motor control tasks do not just fall within the scope of the self-monitoring function of consciousness, but appear to necessitate it. The octopus's lack of internal somatic landmarks potentially deprives it of dependable mechanisms for fine-grained recognition and control of its appendages. In severely deafferented humans, who are likewise deprived of neural pathways for interoceptive monitoring and motor control, consciousness has been demonstrated to be not just a compensatory but an alternative mechanism for carrying out these functions. By contrast, the counterparts of the aforesaid functions in the octopus are executed by operations which may not be conscious at all—or if conscious, may not be causally efficacious. The following sections will examine a number of processes that instantiate the various aspects of the monitoring function, but are possibly unconscious. Those that exemplify self-recognition and behaviour updating or

correction will be discussed first, due to their functional specificity, before proceeding to the more comprehensive capacity for somatic awareness.

#### *7.4.1 Chemical mechanisms for arm recognition*

The octopus's lack of proprioception and its cannibalistic nature make for a potentially deleterious and maladaptive combination. As octopuses have a tendency to bring objects they grasp to their mouths, often eating them altogether, without mechanisms that enable them to recognize their own arms they are likely to self-cannibalize. Thus, the need for a capacity for self-recognition is heavily underscored in the octopus. In its vertebrate counterparts, a significant component of self-recognition would be attributed to proprioceptive input entering into conscious awareness, but this option is unlikely to hold in the octopus for reasons that will be discussed below. Instead, low-level mechanisms found in the skin and suckers are what are responsible for the octopus's ability to recognize its own arms, whose peripheral location raises doubts as to whether their input enters into the field of consciousness.

In a study conducted by Nesher et al. (2014), it was discovered that chemical mechanisms found in the skin and suckers prevent octopuses from grasping—and potentially eating—their own arms. The suckers on the octopus arms are low-level motor effectors that produce only reflex output; an octopus sucker will grasp and adhere to whatever surface it comes into contact with, unless the reflex is interrupted by an inhibitory factor. This grasping reflex, along with anatomical hyper-redundancy and lack of proprioception, is potentially detrimental to coherent behaviour: if the arms come into contact with each other, and the reflex is uninhibited, then the arms would inevitably grasp each other. Yet, such interference does not ordinarily occur in normally behaving octopuses.

A significant finding of the study was that suckers on amputated arms did not grasp any surface that had octopus skin applied to it. When presented with Petri dishes that were partially covered in octopus skin, the suckers of the octopus's receiving arm would avoid the skin altogether. However, suckers on the same arm would grasp exposed portions of the dish; this is possible because suckers are controlled at the level of the individual sucker ganglion. Similar responses were observed when the octopus was presented with an amputated arm: the suckers would not grasp the skin of the amputated arm, but would adhere to skinless areas of it. Further tests conducted using Petri dishes that were coated with a compound containing chemical extracts from octopus skin confirmed the presence

on the skin of a chemical that inhibits sucker reflexes. Due to the dilution of the skin extract, the reflex was not completely suppressed, and the octopus was able to grasp the Petri dish. Furthermore, the suckers grasped dishes with lower concentrations of the chemical more firmly than they did dishes with higher concentrations. These results led to the conclusion that the concentration of the inhibitory chemical affected the strength of the suckers' grasping force.

An even more significant finding was that when presented with amputated arms, intact octopuses were able to distinguish between those that were their own and those sourced from conspecifics. Arms taken from conspecifics were grasped at the skinless areas, and brought to and kept in the mouth, indicating they were regarded as food objects. On the other hand—with a few exceptions—the octopuses did not bring their own amputated arms to their mouths. Significantly, however, when presented with amputated arms whose skin had been completely removed—whether they were their own or those of conspecifics—the octopuses brought them to their mouths and did not take them away. These observations provided further confirmation that octopus skin contains mechanisms that enable the animal to identify its appendages through the use of chemical signals.

Another interesting result of the study was the disparity in the responses of the suckers of intact octopuses and those of amputated arms. The latter consistently demonstrated the results detailed above, i.e., that they would refrain from grasping the arms presented to them, but intact octopuses would randomly grasp amputated arms even though they had skin on them. Nesher et al. (2014) interpret these results as suggesting that centrally issued motor commands may be able to override the peripheral mechanisms that inhibit the sucker grasping reflex.

There are a number of interesting points to consider about how the octopus recognizes its own arms. To begin with, the mechanisms responsible for this capacity are chemical elements in the skin and suckers, and not neuro-psychological processes. Furthermore, this form of self-recognition is exogenous, in that the activation of the operations underpinning it is dependent on contact with stimuli. Rather than being endogenously triggered operations that enable the octopus to interoceptively and immediately recognize its own arms, chemical self-recognition is more appropriately described as a set of processes that inhibit reflex responses that would otherwise have caused the arms to be treated as foreign objects. Self-recognition on the basis of chemical mechanisms can thus be characterized as stimulus-dependent and exafferent—and not intrinsic and persisting, as it is when it has neural or cognitive substrates.

Significantly, octopus self-recognition appears to lack an interoceptive component, which is unsurprising considering its lack of proprioceptive and somatotopic mechanisms. Nesher et al. (2014) interpret the infrequent yet attested tendency of intact octopuses to grab their own arms as central overriding of peripheral control, but admit that such a behavioural phenomenon has not yet been thoroughly researched. One possible explanation for this unusual behaviour would be a temporary malfunction of the self-recognition mechanisms; after all, biological operations are not foolproof. Another possibility would be rivalry between the central and peripheral motor control centres, not unlike the A-not-B error or the key-ring test, which were discussed in Chapters 3 and 7 respectively. While the explanation remains an open empirical question, the persuasive conclusion that can be drawn is that the octopus may have no “back-up” mechanisms for recognizing its arms in case the chemical mechanisms fail. Had the octopus been capable of proprioceptively monitoring its arms, self-adherence can be expected not to occur at all: not only does it interfere with the octopus’ movements, but it can potentially lead to extremely detrimental behaviours such as self-cannibalization, and as such must be avoided.

In the octopus, reflexes and peripheral mechanisms with self-recognition functions are activated only when they encounter stimuli, and as such are not capable of tracking the environment offline. Any conscious experience that may accompany their operations would be parasitic on occurrent stimulation, and cannot arise when the underlying physical substrates are unstimulated. However, as a consequence of their peripheral location and low-level nature, the output of self-recognition mechanisms is not likely to reach the brain, but remains within the arm nervous system. This in turn raises the question of whether self-recognition in the octopus is conscious at all.

In the previous chapter, two possibilities were presented regarding the structure and substrates of octopus consciousness. The mechanisms responsible for generating consciousness may be found either solely in the brain or in both the brain *and* the arms, with the latter entailing that the arms are capable of supporting independent conscious fields. If the former is true, so that consciousness subsumes only those processes that make it to the brain, then octopus self-recognition—which arises due to low-level, stimulus-dependent, peripheral chemical responses—cannot be conscious. This conclusion undermines the claim that the capacity for self-recognition is reliant on consciousness, as it holds that self-recognition in the octopus takes place outside of consciousness. On the other hand, if the arms have idiosyncratic consciousness-generating mechanisms, then self-recognition is likely to have a conscious component. Such conscious experience would

certainly be of the primary or stimulus-dependent, non-reflexive sort; even though it were conscious, chemical self-recognition would lack the introspective features that subserve the monitoring and behaviour updating functions characteristic of more sophisticated forms of consciousness.

Conscious *chemical self-recognition* differs from *proprioceptive self-recognition* in a number of important ways. Whereas proprioceptive self-recognition is persisting and does not necessarily require sensory stimuli to be activated, chemical self-recognition is transient and stimulus-dependent. Consequently, chemical self-recognition does not translate into a capacity for interoceptive recognition of the arms in the absence of stimulation. However, the most significant conclusion that can be drawn about chemical self-recognition in the octopus lies in the way it is conscious: it may *have* a conscious component, but does not arise *as a result* of consciousness.

Another vital point to consider is that the exafferent nature of octopus self-recognition is sufficient to deny it cognitive status. This is again due to the stimulus-dependence of its underlying mechanisms, which render chemical self-recognition not as a cognitive process, but as a merely reactive routine. Even when given that octopus cognition is comprised of non-redundant brain-based and arm-based components, it does not follow that self-recognition in itself is cognitive. It may be recruited by arm-based cognitive processes, or may be involved in more complex brain-based ones, but such participation does not entail that it intrinsically maintains its own cognitive status.

Thus far, it has been argued that the ascription of self-recognition to consciousness as a causally efficacious feature that enhances an organism's adaptive success fails in the octopus. As a consequence of its neural architecture, the octopus does not support proprioceptive self-recognition, and the form of self-recognition that it does have is not causally *dependent* on consciousness. Furthermore, in other species, self-recognition is usually regarded as a cognitive capacity, but in the octopus it may altogether be non-cognitive.

However, there is yet another type of self-recognition, i.e., the more sophisticated capacity for *exteroceptive self-recognition*. It must thus be asked whether the octopus is endowed with this capacity, and if so, how it relates to consciousness. If Neshet et al. (2014) are correct, and the central brain is indeed able to override the peripheral chemical self-recognition mechanisms and allow the octopus to grab its own arms, two implications arise. First, the octopus may be unable to visually recognize its arms as its own, as suggested by its poor performance in mirror self-recognition tests (Mather and Kuba 2013). Second, self-

adherence is evidence that chemical self-recognition operations do not reach the brain. What, then, does this tell us about exteroceptive self-recognition in the octopus?

In organisms with fully integrated nervous systems, exteroceptive and proprioceptive forms of self-recognition usually inform each other. However, there are cases in which one or the other breaks down, resulting in the failure to recognize one's own body or parts of it, or the misperception that one's own body or parts of it are not one's own. Commonly cited examples of the malfunction of self-recognition mechanisms include the *rubber hand illusion*, and extensive deafferentation such as that of Ian Waterman (see Chapter 7). The rubber hand illusion consists of having the subject insert her hand into a box to obscure it from view; the eponymous rubber hand is then set in front of her. Both the subject's hand (which she cannot see) and the rubber hand (which is in plain sight), are then touched at the same time and in corresponding places. After this has gone on for some time, the illusion arises: even though tactile stimulation to her own hand ceases, when the subject sees the rubber hand being touched, she "feels" it on her hand. In this case, proprioceptive self-recognition fails temporarily. As discussed in detail in the previous chapter, Waterman controls the movements of his body by effectively treating them as perceptual objects; he must visually monitor his movements in order to ensure that his motor trajectories are on track. Waterman himself has stated that his movements always go off-kilter if he cannot see what he is doing.

The consequences of compromised proprioceptive self-recognition are demonstrated by the rubber hand subject's incorrect integration of visual and tactile input, Waterman's movements "misfiring," and the octopus's failure to inhibit self-adherence. If the rubber hand looks sufficiently realistic, and is positioned well, it is not difficult to see how the subject can visually mistake it for her own hand. What makes the results of this experiment highly compelling is that they run counter to the expectation that proprioceptive signals—which would be expected to be more reliable due to their immediacy—would counteract or override visual stimuli, and prevent the subject from succumbing to the illusion. In Waterman's case, visual, i.e., exteroceptive self-recognition is indispensable to his control over his movements; when he is unable to see his limbs, he is unable to move them. If he is subjected to experimental conditions such as those surrounding the rubber hand illusion, and wherein the copies of his effectors that he is presented with are highly realistic, he would presumably be unable to identify his real hand. This is due to his having no sensory means besides vision by which to recognize his body parts. In Waterman, exteroceptive self-recognition compensates for the absence of its proprioceptive



counterpart, thus demonstrating that cognitive routines—especially motor control—which depend on both types of self-recognition can continue to function even in the absence of one. Self-recognition is most reliable when it is standing on both proprioceptive and exteroceptive legs. However, under certain conditions, it is forced to stand on just one—and this is as far as it can go without debilitating cognition. Thus, it is important to ask whether the octopus is capable of exteroceptive self-recognition.

The findings of Byrne et al. (2006a) and especially those of Gutnick et al. (2011) suggest that the octopus is capable of visually recognizing its own arms. In object retrieval tasks, octopuses tend to use the arm or arms which lie directly in their line of sight (Byrne et al. 2006a). In the maze test conducted by Gutnick et al. (2011), it was observed that octopuses would position themselves in order to get a better view of the food reward. Once they were properly oriented, the octopuses would then reach into the maze with a single arm to retrieve the food. Importantly, the octopuses performed markedly better when they could see their arms through a clear maze, than when they had to complete the same task with an identical opaque maze. Similar to Waterman’s case, it appears that even though the octopus brain does not receive proprioceptive peripheral feedback, it can nevertheless exert a certain extent of control over arm movements. Furthermore, it also suggests that octopuses can visually, and thus exteroceptively, recognize their own arms.

However, the fact that octopuses sometimes grab their own arms might appear to be a slight obstacle in the way of the conclusion that they are capable of exteroceptive self-recognition. As discussed earlier, without proprioceptive and chemical self-recognition, only visual self-recognition can prevent such a deleterious action from being carried out. If the octopus can indeed exert some central control over its arms, as Gutnick et al. (2011) propose, then why are there instances of potentially injurious self-adherence behaviour? The answer may simply be that exteroceptive self-recognition mechanisms are imperfect, and are thus susceptible to occasional errors, i.e., failure to prevent the instances of self-adherence that do occur. Furthermore, self-adherence is infrequent enough to be unequivocally considered atypical behaviour in the octopus. As such, it does not compromise the possibility that octopuses can exteroceptively recognize their own appendages.

#### *7.4.2 Behaviour updating*

Ensuring that motor trajectories are correct is a crucial component of behaviour, and is another routine subsumed by the self-monitoring function of consciousness. Yet, as

extensively discussed in Chapter 3, much of the octopus's motor control operations are relegated to the periphery. Like chemical self-recognition, the dynamical neuromuscular operations in the arms that are responsible for supplying the kinematic parameters of movement may be accompanied by conscious experience—depending on how the structure of octopus consciousness is construed—but they are not an outcome of consciousness. (Because of the detailed treatment dynamical arm motor control has already received in the first part of the thesis, there is no need to revisit it here.)

Once again, the findings of Gutnick et al. (2011) prove to be a trove of insights regarding the functional role consciousness may play in the cognitive economy of the octopus. As completion of the maze test called for the use of novel movements, the experiment effectively involved a learning component. The observable actions indicating that the octopuses had learned to perform the task were their positioning themselves to get a good view of the food reward, and changing motor strategies by which they retrieved it. Initially, the octopuses used *straight* movements, which involved first inserting the arm into the main compartment, then propagating a bend that allowed it to enter the chosen compartment. However, as the trials progressed, *search* movements characterized by “crawling and probing” (Gutnick et al. 2011, 462) were used more frequently than straight ones, and produced higher success rates.

While both motor strategies are stereotypic motor components that are incorporated into the octopus's natural movements, they differ in their underlying motor control routines. Straight movements are centrally controlled: they are activated by central, global commands that prescribe the speed and general trajectory of the movement. Due to their feed-forward nature, sensory feedback is not incorporated into their command sequence. In contrast, search movements are controlled from the periphery, and directed by reflexes responding to tactile and chemical stimuli. It is thus significant that the octopuses resorted to using search movements more often, as they were deprived of both chemical and tactile cues in the maze task.

Search movements, which are used in hunting and exploratory behaviours such as the rather misleadingly named technique of *speculative hunting* (wherein the octopuses pounce on a structure under which prey is likely to be hiding, such as a rock or a coral, and feel underneath it with their arm tips), are normally controlled from the periphery, with “little or no central control” (Gutnick et al. 2011, 462). Yet the results of the maze test indicate that in that particular context, the very same motor technique was controlled from the brain. This finding is crucial, as it indicates that under abnormal circumstances in which

stimuli used in typical peripheral motor control routines are suppressed, central control of search movements—and perhaps other arm movements—can be implemented. More specifically, arm movements can be guided visually and without the benefit of proprioceptive feedback and somatotopic representation.

Comparably, in Waterman's case, motor control requires visual guidance and focused attention on the appropriate effectors and their motor trajectories: because of his impairment, he is "required to pay an *inordinately high degree of attention* to his body" (Gallagher 2005, 45, emphasis mine). As such, control of his voluntary or deliberate movements is always conscious. His case is a direct parallel to the octopuses in the maze test, which had to rely on visual input to ensure that their motor trajectories were on the right path. Like Waterman, for the octopuses to direct their arms through an atypical structure, they would have had to pay close attention to them throughout the duration of the task's performance.

Central control of the arms entails not only exteroceptive self-recognition, but also exteroceptive motor control—both of which entail the causal participation of consciousness. In the absence of proprioception and somatotomy, it provides the means and mechanisms necessary for monitoring the physical condition of the body and its parts, and for calculating how to adjust the motor trajectories of the relevant effectors. The latter is possible due to the fact that one of the functions attributed to consciousness is serving as an offline or decouplable model of actions and their consequences on the physical environment, thereby allowing the organism to predict plausible future outcomes. Thus, it can be concluded that the behaviour updating component of the self-monitoring function of consciousness holds in the octopus.

Or does it? It must be remembered that under normal circumstances, arm movements are controlled peripherally. Furthermore, as they are controlled and guided by reflexes, search movements are low-level actions, in contrast to complex actions such as full-arm extensions, which have to be activated by a central command transmitted through the axial nerve cord. As such, updating search movements that are controlled via their normal pathways can take place only if the reflex mechanisms are coupled to the stimuli afforded by the surfaces encountered by the arm concerned. The issue of whether peripheral motor control centres and sensory receptors contribute to consciousness has been discussed in the previous section; because the same concerns and arguments hold in the present context, there will be no need to repeat them. As was discussed in Chapter 7, the question

of whether peripherally controlled search movements are conscious or not depends on the number of conscious fields an octopus has, and where their substrates are located.

If it is accepted that the arms support conscious experience, then search movements may have a qualitative component. Yet because their underlying control mechanisms are stimulus-dependent and too low-level to support reflexive or self-updating functions, the conscious experience accompanying them may not be causally efficacious. A similar conclusion holds if it is presupposed that the octopus's consciousness mechanisms are found solely in the brain. As information from the reflexes remains within the confines of the peripheral nervous system, search movements may not be conscious at all. In this case, octopus consciousness would not subsume interoceptive experience of the arms, much less have causal influence on controlling their movements.

The overall picture is peculiar, even counter-intuitive. Under normal conditions in the wild, arm control takes place peripherally. But when octopuses are placed in highly unusual experimental settings, it is possible for them to switch to an alternative, centrally governed control routine (Godfrey-Smith 2013). It is when the latter is in play that the causal efficaciousness of consciousness is brought to the forefront. The conclusion that can be drawn is that octopus consciousness can serve as a motor control mechanism, thereby functioning as a means of updating behaviour, but conscious control of the arms is not a typical motor routine.

#### 7.4.3 *Somatic awareness*

While the refference problem is one that confronts organisms with sensorimotor capacities in general, in the octopus it would have been especially intractable had it not been for the unique features its nervous system acquired over its evolutionary development. Without the benefit of systems that provide mechanisms for interoceptive somatic monitoring, an octopus could potentially lack awareness of the movements of its arms. In turn, without a reliable capacity for interoceptively keeping track of its own body and movements, the octopus would be highly susceptible to deleterious behaviours such as self-adherence and self-cannibalization. It thus comes across as paradoxical that interoceptive monitoring is sparse in the octopus—in which the need for accurate and reliable monitoring mechanisms is underscored by its anatomical and motor hyper-redundancy and potentially unlimited degrees of freedom in the articulation of its arms.

Presupposing the neuralization of consciousness, i.e., the claim (discussed in Chapter 7) that conscious experience is parasitic upon neural states, it can be expected that

the octopus's lack of proprioception translates into the absence of interoceptive awareness about the arms from its main, brain-based conscious field. Due to its comprehensiveness and complexity, brain-based consciousness is associated with goal-directed behaviour, which in turn is underpinned by somatic awareness. It thus seems counter-intuitive that interoceptive information about the state of the arms would be excluded from brain-based consciousness, either completely or partially, but to an extent that it is rendered causally impotent with respect to motor control. Yet, this is the very conclusion the neuroanatomical and behavioural evidence points toward. That is to say, there are reasons to believe that the octopus has the capacity for somatic awareness—even in the absence of causal inefficaciousness of proprioception and somatotopic representation.

When somatic awareness is cashed out to include self-reflexive features, then it must be understood as a conscious cognitive capacity whose substrates are located in the brain. While the peripheral mechanisms that enable the octopus to identify its own body parts and detect its somatic boundaries may be capable of generating qualitative states, they are not sophisticated enough to scaffold a sense of agency. That is to say, while the arm may be able to produce low to intermediate behavioural responses to stimulation, the functional constraints on its neural mechanisms preclude higher-level conscious states of the sort that would enable it to reflexively recognize itself as an experiencing subject.

Another salient feature of somatic awareness in the octopus that sets it apart from familiar models would be its dependence on an exteroceptive component, namely visual information. Without conscious proprioceptive feedback, the octopus's visual experiences of its own arms would be the only reliable sources of information about their state and motion. As discussed in the previous section, the role played by visual feedback in motor control is likewise emphasized.

The downplaying of interoceptive states and the emphasis on exteroceptive ones make for an exceptional and unexpected form of somatic awareness. While consciousness is a major player, both in the octopus's awareness of its own body and its motor control operations, its structure is highly unusual—even paradoxical—in that it excludes proprioception, which is usually considered to be an indispensable component of the conscious field. Interestingly, what the evidence suggests is that, in the octopus, visual feedback is responsible for a number of recognition, monitoring, and control functions that are usually relegated to interoceptive operations.

## **7.5 Conclusion: Functions of octopus consciousness**

The octopus's ability to switch from peripheral to conscious central motor control over the arms is presumably an adaptive function. Conscious motor control is biologically costly, especially in the case of the octopus, with its hyper-redundant, soft body with no proprioceptive guideposts. While there is compelling evidence to believe that the octopus has a persisting conscious field, in that its nervous system is capable of supporting subjective experience, exerting extensive conscious control over its arms would prove to be neurally taxing. In a direct parallel to the functional decomposition of its nervous system, conscious control mechanisms in the octopus are perhaps used mainly for global control and goal-directed behaviour, e.g., selecting behaviours to carry out, activating and terminating them, and orientation towards stimuli. Conscious control of the arms as the dominant routine would come at an exorbitant neural cost, and furthermore would be inefficient due to the sparseness of the octopus's interoceptive monitoring mechanisms. Thus, the functional roles of consciousness in the octopus may have evolved isomorphically with its nervous system.

The two models of the decomposition of the structure of octopus consciousness both challenge the monitoring function of consciousness in distinct but related ways. The central consciousness model would retain the monitoring function and its various components, albeit with one critical modification: the diminished role of interoceptive monitoring and control operations. Consequently, a single, brain-based conscious field would have to be causally efficacious; otherwise, deleterious and potentially fatal impairments to both the octopus's bodily monitoring and motor control functions would ensue.

An even more interesting picture emerges if the distributed consciousness model is presupposed. Here, brain-based and arm-based conscious fields would have different causal statuses. Brain-based consciousness, which is an indispensable mechanism that makes goal-directed behaviour in the octopus possible, would without a doubt be causally efficacious. Like Ian Waterman's methods of alternative motor control, brain-based consciousness must be capable not only of monitoring movements and keeping them on track but also of overriding normal motor routines when abnormal conditions make their execution difficult or impossible. However, brain-based consciousness is puzzling because it must carry out these functions without the benefit of proprioceptive feedback and fine-grained control over the arms. Arm-based conscious fields, on the other hand, would subsume the tactile, chemical, and proprioceptive states of the appendages they are

localized in. But unlike their more sophisticated central counterpart, they are but of a primary, stimulus-dependent nature. Hence, the causal efficaciousness of arm-based consciousness is limited to peripheral motor control. Although the operations responsible for providing the kinematic parameters of movement may be accompanied by conscious states, they would not be subsumed under the main conscious field; or if they were, they would not be fine-grained enough to allow for detailed control of specific arms.

The structure of octopus consciousness poses an interesting challenge to the monitoring function, which is considered to be the evolved adaptive role of consciousness. In this light, consciousness is viewed as a mechanism that equips an organism with the capacity to model and monitor its condition as it acts on and is acted upon by the external world. It is thus unsurprising that interoceptive states, particularly those generated by proprioception and kinesthesia, are vital components of the conscious field. The indispensability of interoception is brought to the fore when consciousness is counted among motor control operations. It is thus interesting and unusual that proprioceptive information about the arms is significantly downplayed in octopus consciousness. Instead, the various constituent operations contributing to the monitoring function are carried out by systems that are likely to be excluded from the causally efficacious conscious field by virtue of their neuroanatomical location.

The atypical structure of octopus consciousness thus precludes generalizations regarding the adaptive functions of consciousness. In doing so, it also raises questions regarding the right of consciousness to remain in the explanatory toolkit of cognitive science. As it is, consciousness is an embattled notion that has had to fend off the onslaught of blows from behaviourist, reductionist, and eliminativist corners. With the addition of the octopus to its interlocutors, the following question is raised: if the functions attributed to consciousness can be carried out by non-conscious operations, or by processes that are accompanied by a non-causally efficacious conscious component, does consciousness have a *universal* functional role that enhances the biological success of the organisms in which it is instantiated? While the ontological and explanatory status of consciousness is relatively more stable today than it was in the past, questions still remain about its causal contributions to cognition.





## **PART IV**

### **COGNITIVE SCIENCE GETS SEA LEGS:**

## **CONCLUSION**

The discussions presented in this thesis show that extant models of the mind, which have been based on vertebrates, are inadequate to account for the octopus, a neurally “atypical” creature with highly sophisticated cognitive and behavioural capacities. Cognitive science up to the present rests largely on the study of human and various forms of vertebrate intelligence, and as such has extensive familiarity with how centralized nervous systems generate and subserve advanced intelligence. However, it is not as well-equipped to account for cognition in invertebrate species. Consequently, where invertebrate cognition is studied, it is usually analysed using an explanatory toolkit designed for vertebrates. As such, it is rendered susceptible to false negatives, i.e., to denying cognitive status to a neural or behavioural process or phenomenon when it may actually be genuinely cognitive.

A well-known example of denial of cognitive status to a complex form of invertebrate behaviour revolves around ants’ removal of dead conspecifics from their nests. Such behaviour can be naively interpreted as requiring various forms of advanced cognitive processing, e.g., recognition that dead ants must be disposed of properly in order to maintain the hygiene of the nest. However, it has been demonstrated that carcass disposal in ants is fully dependent on chemical stimuli, in the form of the oleic acid emitted as the body decomposes. In this case, cognitive status has been denied to the aforesaid behaviour on the basis of its being stimulus-dependent, and under more stringent criteria, non-representational (Sterelny 1995).

It must be noted the present discussion does not aim to challenge the denial of cognitive status in this particular case. Instead, the objective is to point out that such a dismissive approach is commonly taken when studying invertebrates—and that it is not always appropriate as it can lead to inaccurate conclusions. In certain cases, attributing cognition stands out as more plausible than denying it. This is especially true in octopuses, whose behavioural complexity is firmly grounded in neural substrates that are homologous to, or at least functionally comparable with, those of vertebrates that have been accepted as genuinely cognitive. In particular, these are the brain-based neural structures subserving memory and learning. While the octopus nervous system as a whole is highly distributed, the lobes of the central brain are considerably integrated, and thus exhibit the anatomical conditions required for domain-general cognitive capacities to arise. Nevertheless, it is important to note that this lobular integration does not entail centralization of the nervous system—especially when the neuroanatomical components responsible for the major domains of visual processing and motor control are excluded from the octopus's brain. Thus, the cognitive architecture that arises from the organization and structure of the octopus nervous system is one whose output and capacities are comparable to those of vertebrates, yet these are generated through mechanisms and processes that differ radically from those responsible for vertebrate cognition.

The distribution of labour within octopus cognition provides strong empirical support for something that traditionalists have known all along: that a considerable degree of neuroanatomical integration is required in order to generate sophisticated cognitive capacities, especially those that rely on stimulus-independent information in order to give rise to adaptive behaviour. Nevertheless, it must be pointed out that the theoretical possibility remains open that these cognitive capacities can also be realized in organisms whose nervous systems are highly distributed.

Octopus cognition also stands as evolved and empirical proof for the claim that some strands of embodied cognition have been arguing for: namely, that certain cognitive domains can be realized through the use of decentralized mechanisms without compromising the cognitive and behavioural capacities of the overall system or organism. The octopus directly demonstrates that motor control is an example of one of these domains. Thus, the octopus is a highly successful biological instantiation of the extent to which a cognitive system can be decentralized without becoming brittle or functionally unstable.

It is not just the decentralization per se of the octopus nervous system that merits an alternative model of cognition. More importantly, this decentralization precludes the realization of a number of neuropsychological mechanisms traditionally considered as vital to cognition. However, it also allows for “alternative” pathways by which comparable cognitive output can be produced. Thus, the octopus calls into question our understanding of how cognition takes place, especially with regards to the neural and somatic mechanisms by which cognitive processing arises.

The importance of the octopus to the cognitive and brain sciences lies in its departure from familiar, vertebrate-based models of cognition on structural, functional, and explanatory grounds. As the octopus is on a par with vertebrates in terms of psychological and behavioural capacities, it necessitates a model of cognition that is better suited to its cognitive architecture. It is of the utmost importance to emphasize the similarities between vertebrate and octopus cognition, as they are what justify the genuine need for an “octopus-friendly” model of the mind. If the cognitive output exhibited by the octopus had diverged significantly from that of uncontroversially cognitive vertebrates, then it could easily be dismissed as what Kim Sterelny (1995) refers to as “vacuum behaviours” or stimulus-dependent actions, regardless of their complexity. But as octopuses have been established to be psychologically and behaviourally vertebrate-like—not just superficially but substantively—the conclusion that can be drawn almost incontrovertibly is that the octopus nervous system instantiates another way in which this particular kind of cognitive sophistication can arise.

An octopus-based model of cognition would be one that exhibits functional decentralization, especially with regards to motor control. It would also be an ontologically hybrid one, in that it can cleanly distinguish between cognitive routines that are representation-using and those that are dynamical. More importantly, it would have to demonstrate how cognitive operations that are instantiated in diverse formats interact in order to process information and generate adaptive behaviour. While the endeavour to formulate a model of cognition that is well-suited to the octopus is a valuable move that can expand our knowledge of how the mind works, in itself it is a narrow project. Where, then, lies its broader significance?

One of the first disciplines to reap the benefits of an octopus-based neurocognitive model would be comparative cognition. Even though the octopus is very vertebrate-like in terms of its cognitive and behavioural capacities, the fact remains that it is an invertebrate;

that is to say, the functional decentralization of its nervous system is a feature that is characteristically invertebrate. When working with a decentralized model of cognition, the first step to take is to identify the anatomical structures that contribute to cognitive processing and determine how cognitive labour is distributed among them. As nervous systems vary across species, so will the substrates of species-typical forms of cognition. Studying invertebrate cognition through the lens of vertebrate-based models runs the risk of generating false negatives, in large part due to the vast differences between invertebrate and vertebrate cognitive architectures. Thus, the availability of an octopus-based cognitive model can be used as a methodological point of reference for studies of intelligence in invertebrates.

The ways in which certain cognitive routines are realized in the octopus due to its decentralized nervous system bear striking similarities to their counterparts in non-neurotypic humans. For instance, the lack of central proprioceptive and somatotopic mapping mechanisms in the octopus is comparable to deafferentation in humans, while the distribution of motor control responsibilities between the brain and the arm nervous system functionally resembles the split-brain syndrome. What these neurophysiological resemblances between normal octopuses and non-neurotypical humans have in common is that accounting for them requires departure from familiar explanatory tools and strategies. Importantly, while incomplete transfer of information within the vertebrate nervous system makes conditions like the split-brain syndrome and deafferentation stand out as non-neurotypic, in the octopus incomplete transfer of information is a matter of normal neuroarchitectonic fact. As such, the causal structure of a number of cognitive routines in the octopus—especially those for motor control—demonstrate how adaptive or goal-directed behaviour can be produced under what are atypical or abnormal neural conditions for vertebrates. In providing different ways of understanding how cognitive processes are realized, the octopus can help the cognitive and brain sciences expand their explanatory territory by presenting them with “alternatives” to familiar causal pathways along which nervous systems are known to function.

The neuroanatomical organization and ensuing cognitive architecture of the octopus bring in their wake important implications for theoretical and empirical approaches to consciousness. While there is still considerable hesitance within philosophy and neuroscience to accept consciousness as a genuine explanatory tool, it is nevertheless a psychological phenomenon that cannot be easily dismissed. Furthermore, there is

increasing awareness and acknowledgment that consciousness has cognitive and adaptive value, especially with regards to motor control. Over and above its intuitive appeal, the explanatory value of accepting the existence of consciousness lies in its being regarded as a reflection of how subjective experience is affected by neurobiology. To be more precise, consciousness is held to demonstrate the experiential correlates of the physical condition of the nervous system.

The octopus has been identified as a creature whose nervous system is likely to generate and support consciousness, in the sense of persisting first-person subjective experience. Accepting this notion allows us to probe—albeit speculatively—into a peculiar type of *creature-consciousness*—i.e., consciousness as it is instantiated in a given species—that does not exhibit the features that are believed to be responsible for the cognitive and adaptive functions attributed to consciousness in general. The treatment octopus consciousness has received in this thesis demonstrates that it differs significantly from its human and other vertebrate counterparts in terms of structure and, consequently, function. As the issue of consciousness is a fragile one, in that it is still at risk of being dismissed or bypassed in favour of explanatory mechanisms that are less resistant to direct observation, it is of the utmost importance to note that the discussions in this chapter do not aim to discredit the existence or the causal efficacy of consciousness. Rather, they should be regarded as endeavouring to further reduce vertebrate bias in studies of the mind, particularly by demonstrating that the functional roles played by consciousness can vary across species.

As an outcome of this causal diversity, the various types of creature-consciousness may interact with the nervous and cognitive systems of their respective species in ways that differ from humans and vertebrates. In the same way that caution must be exercised when using behaviour-based approaches to attribute consciousness in general to non-human animals, the task of identifying the cognitive and adaptive value of various types of creature consciousness calls for extreme care. When not accompanied or complemented by information about the neurophysiology and anatomy of the species in question, determining the species-specific functions of consciousness becomes highly susceptible to false negatives and false positives alike (Andrews 2015).

False positives arise when consciousness is held to make causal contributions to certain cognitive routines or forms of adaptive behaviour, when in fact these are carried out through the use of non-conscious mechanisms or processes, e.g., chemical self-recognition in the octopus. While such cognitive operations may indeed have a conscious component,

its causal contributions might not resemble those made by their counterparts in human cognition. False positives are likely to occur as a result of anthropomorphism, when certain behaviours that are regarded as indicative of consciousness in humans are observed in other animals, and inferred to be governed by the same mechanisms, down to the causal roles attributed to their qualitative components. On the other end of the spectrum, false negatives entail failing to recognize that certain cognitive processes or behaviours, such as Ian Waterman's visually-directed motor control schema, require the causal participation of consciousness. However, false negatives are extremely difficult to detect, as they require a direct and incontrovertible means of ascertaining the substantive involvement of consciousness.

Taken collectively, the issues about octopus consciousness that were addressed in this thesis point to neuropsychological factors that inter-species studies of consciousness must be aware of. The acceptance of consciousness as a legitimate theoretical and empirical explanatory tool lies in establishing its genuine causal contributions to an organism's biological success and cognitive capacities. As such, studies on animal minds that focus on identifying the biological and adaptive functions of consciousness must seek to avoid erroneous generalizations, which generate brittle and easily falsifiable claims that can potentially undermine the broader research program of investigating the causal significance of consciousness.

By presenting the structure and functions that consciousness in the octopus is likely to exhibit, given the features of the animal's nervous system, this thesis provides an example of the extent to which species-specific subjective experience can diverge from the models of the mind that cognitive science is currently familiar with. The aforesaid discussions also demonstrate that an analysis that superimposes a human-based template of consciousness on a creature whose nervous system radically differs from that of vertebrates will almost certainly lead to faulty conclusions. Due to space and content constraints, the treatment of subjective experience in the octopus in this thesis is less of a didactic tale that provides detailed instructions for investigating consciousness in invertebrates, but more of a cautionary one that warns that failure to recognize that subjective experience can interact with various neurocognitive systems in species-specific ways can compromise understanding of how it contributes to a creature's cognitive sophistication and biological success.



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