Body models in humans, animals, and robots

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Abstract

Humans and animals excel in combining information from multiple sensory modalities, controlling their complex bodies, adapting to growth, failures, or using tools. These capabilities are also highly desirable in robots. They are displayed by machines to some extent—yet, as is so often the case, the artificial creatures are lagging behind. The key foundation is an internal representation of the body that the agent—human, animal, or robot—has developed. In the biological realm, evidence has been accumulated by diverse disciplines giving rise to the concepts of body image, body schema, and others. In robotics, a model of the robot is an indispensable component that enables to control the machine. In this article I compare the character of body representations in biology with their robotic counterparts and relate that to the differences in performance that we observe. I put forth a number of axes regarding the nature of such body models: fixed vs. plastic, amodal vs. modal, explicit vs. implicit, serial vs. parallel, modular vs. holistic, and centralized vs. distributed. An interesting trend emerges: on many of the axes, there is a sequence from robot body models, over body image, body schema, to the body representation in lower animals like the octopus. In some sense, robots have a lot in common with Ian Waterman—“the man who lost his body”—in that they rely on an explicit, veridical body model (body image taken to the extreme) and lack any implicit, multimodal representation (like the body schema) of their bodies. I will then detail how robots can inform the biological sciences dealing with body representations and finally, I will study which of the features of the “body in the brain” should be transferred to robots, giving rise to more adaptive and resilient, self-calibrating machines.

1 Introduction

Ulric Neisser distinguishes five different selves: the ecological self, the interpersonal self, the extended self, the private self, and the conceptual self (Neisser, 1988). The high-level facets of the self—accessible to consciousness, incorporating linguistic information etc.—have been receiving relatively more attention. However, here I will focus on the lowest level—the ecological or sensorimotor self or the “body schema”—which constitutes a key foundation for the rest. The description by (Graziano & Botvinick, 2002) nicely expresses the sensorimotor, multimodal, and spatial nature of the body representations I focus on: “implicit knowledge structure that encodes the body’s form, the constraints on how the body’s parts can be configured, and the consequences of this configuration on touch, vision, and movement.”
There first key question I want to address is: What are the fundamental differences in which animals, humans, and robots represent their bodies. While the main goal is to get understanding of the mechanisms of “the body in the biological brain”, the “robot world” can be instrumental here in two ways. First, there is a large body of mature mathematical tools for representing kinematics and dynamics, for employing these representations in movement planning and control, as well as for learning models of physical systems (system identification). These constitute in some sense the “ideal world”, a neat mathematical description of the problem, which opens up a useful perspective on the body models that evolution has arrived at. Second, robots can serve as embodied computational models of biological body representations. Humanoid robots possess morphologies—physical characteristics as well as sensory and motor apparatus—that are in some respects akin to human bodies and can thus be used to expand the domain of computational modeling by anchoring it to the physical environment and a physical body and allowing for instantiation of complete sensorimotor loops.

The second key question is: Which properties of the biological "body schema" could be transferred to robots to make them more adaptive and resilient? On one hand, robots are endowed with neatly engineered body models and control algorithms. Yet, in many respects, their performance in commanding their bodies in unstructured environments, adapting to failures or tools etc., is still hugely lagging behind their biological counterparts. Therefore, Section 5 will examine which of the characteristics of the “body in the brain” should robots take on board.

2 Body models – octopus, primates, robots

Biological and artificial agents have very different bodies as well as very different representations thereof. In this section I will look at some of the characteristics of bodies and “brains” of invertebrates, primates, and robots. Reaching will be used throughout as a behavior that requires some form of—implicit or explicit—body model.

The invertebrate brain and reaching in octopus

Unlike in vertebrates, invertebrate species show an enormous diversity in body plans and nervous organization (Marder, 2007) (Zullo & Hochner, 2011). With more complex bodies and nervous structure, there is a tendency toward centralization with formation of a structured cephalic ganglion. Ganglia or their groups become larger and tend to form semi-autonomous systems for sensorimotor control. Brain development in the rostral part of the animal comes also from the presence of distal sensing such as vision. Within the higher nervous system, sensory feedback areas tend to be topographically organized: central ganglia receive projections from various body parts and show a general somatotopy (Walters, et al., 2004) (Vitzthum, Muller, & Homberg, 2002) (Wong, Wang, & Axel, 2002). Interneurons become more common and constitute a key element in processing and integrating information.

The most advanced invertebrate class are the Cephalopods—highly derived mollusks. They feature on one hand the highest centralization of the nervous system. On the other hand, next to the central nervous system (CNS) composed of the brain and two optic lobes, there is a large peripheral nervous

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1The beginning of this section draws heavily on (Zullo & Hochner, 2011).
system (PNS) of the body and the arms. The brain consists of 30-40 interconnected lobes with a high degree of cross-talk; yet, the interconnections appear less elaborate than in vertebrate brains (Young, 1971). Despite the high level of centralization and in contrast to vertebrate and insect brains, there is no obvious somatotopic arrangement in either motor areas or sensory areas.

The most prominent, most intelligent, and with the largest nervous system among Cephalopods is the octopus. The octopus has a unique embodiment: a flexible body and eight arms with virtually infinite degrees of freedom. Brain stimulation reveals that motor control is hierarchically organized into three functional levels. In the higher motor centers located in the basal lobes, microstimulation evokes complex movements which are, however, not somatotopically represented but controlled by parallel overlapping circuits representing individual motor programs. The basal lobes receive inputs from the optic lobes and other sensory centers.

(Yekutieli, et al., 2005) (Yekutieli, Sagiv-Zohar, Hochner, & Flash, 2005) developed a dynamic model of the octopus arm and used it to hypothesize the mechanism of how a reaching movement is generated. Despite the complexity of the arm, they found that in their model only 2 control parameters suffice to fully specify the extension movement of the arm: (i) amplitude of activation signal and (ii) activation traveling time. This hypothesis seems in line with EMG recordings and other evidence from real octopus. Larger amplitudes would result in same kinematics but larger forces, increasing the arm’s stability against perturbations. For reaching directed at a particular target, two additional control parameters are necessary for the orientation of the arm base. Considering both the experimental and the simulation results, (Yekutieli, Sagiv-Zohar, Hochner, & Flash, 2005) speculate that the octopus reaches toward a target using the following strategy:

1) Initiating a bend in the arm so that the suckers point outward.
2) Orienting the base of the arm in the direction of the target or just above it.
3) Propagating the bend along the arm at the desired speed by a wave of muscle activation that equally activates all muscles along the arm.
4) Terminating the reaching movement when the suckers touch the target by stopping the bend propagation and thus catching the target.

There are 3 kinematic control parameters (2 angles for arm base orientation and 1 for movement speed) and 1 dynamic control parameter corresponding to muscle force.

However, the behavioral repertoire of the octopus is greater. (Gutnick, Byrne, Hochner, & Kuba, 2011) prepared a special setup where the octopus has to guide one of its arms through a maze to reach food in one of three branches marked by a visual cue. The octopus is capable of such “hand-eye coordination”. Also, instead of the stereotypical largely feedforward bend propagation, it uses a much slower—but possibly feedback-controlled—“search movement”. Finally, to bring food to the mouth, the arm is bent in a specific way, creating “virtual joints” along it.

Body in the primate brain
It is not in my capacity or my goal to review the structure and function of vertebrate nervous systems. Instead, I will briefly discuss how the body is represented in the brain of primates which include monkeys, apes, and humans. Again, reaching will serve as an example in which a body model of sorts needs to be employed.
The presence of various “body maps” in the primate brain has fascinated scientists and the general public alike, spurred by the account of Head and Holmes (Head & Holmes, 1911) and the discovery of the somatotopic representations (the “homunculi”) in the primary motor and somatosensory cortices (Leyton & Sherrington, 1977) (Penfield & Boldrey, 1937). Neurological conditions and accounts of a whole range of illusions regarding own body perception (e.g., rubber hand illusion, out-of-body experience, apparition) generated both seminal research articles (e.g., (Botvinick & Cohen, 1998), (Lenggenhager, Tadi, Metzinger, & Blanke, 2007)) and public interest. The attention devoted to the representations of the body in the brain has also led to numerous attempts at describing or defining them and proposals of a variety of concepts including superficial and postural schema (Head & Holmes, 1911), body schema, body image, corporeal schema, etc. have been put forth. One characteristic common to all these representations is their multimodal nature: they dynamically integrate information from different sensory modalities (visual, tactile, proprioceptive, vestibular, auditory) (Azañón, et al., 2016), not excluding motor information. However, the concepts of body schema, body image, and many others are umbrella notions for a range of observed phenomena rather than a result of identification of specific mechanisms. The field is thus in a somewhat “chaotic state of affairs” (Berlucchi & Aglioti, 2010), with limited convergence to a common view (Graziano & Botvinick, 2002) (Holmes & Spence, 2004).

Reaching behavior in primates bears some similarity to that in the octopus. A reaching movement has some high-level characteristics like the direction of hand’s movement in space, the extent of the movement (amplitude), the overall duration (movement time), and other parameters such as anticipated level of resistance to the movement (Schöner, Tekülve, & Zibner, 2018). Also, movement generation involves the cooperation between the central and peripheral nervous system. The exact mechanisms of motor control in humans and other primates are still debated (see e.g. (Lisman, 2015)). One view—the equilibrium point theory—posits that high-level descending motor commands modulate the peripheral reflex loops (such as the stretch reflex) and set a desired muscle length (Feldman, 2011). Compared to invertebrates, motor control in vertebrates, specifically mammals and in particular primates, becomes more “cortical” and the motor cortex has the possibility of more direct control over the details of a particular movement, which is likely correlated with the need for dexterous manipulation.

Also, it may not be possible to decouple the movement preparation phase from its execution. The actual movement may be a product of couplings of feed-forward and feedback control that are necessary to understand effects such as the uncontrolled manifold (Scholz & Schöner, 1999) (Martin, Reimann, & Schöner, 2019).

It is also not completely clear whether a prerequisite for a reaching movement is localizing the effector—say the arm / hand—in space first. Through cortical microstimulation, Graziano was able to elicit stereotypical movements in the monkey irrespective of the starting position (Graziano M., 2006). However, (Schöner, Tekülve, & Zibner, 2018) speculate that the stimulation could drive an update of the hand position first which would be subsequently used for the movement generation—in line with (Scott & Kalaska, 1997) who found that neural tuning curves in motor cortex depend on the arm’s kinematic configuration.
In this chapter, I will specifically focus on a task in which localizing own body cannot be circumvented: reaching to own body parts. For example, (Lisman, 2015) notes: “More difficult to imagine is how one can reach one’s ear lobe without visual guidance. This requires knowledge of the position of the target and the position of the limbs. It has only recently become clear that there is indeed a population code that represents hand position (Hauschild et al., 2012), but surprisingly little is known about the muscle and joint signals that allow this computation to be made (Weber et al., 2011).”

Robot body models
The world of robots and their body models is completely different. The first striking difference is that describing it is significantly easier: robot body representations and control schemes are designed by engineers and are thus very transparent and, unlike in the brain, we have complete access to all information. Let us take the iCub humanoid robot as an example. The iCub (Metta, et al., 2010), Figure 1, is a baby humanoid robot that was designed after a 4-year old child—with similar body proportions, kinematic structure and sensorimotor capacities. At the same time, it is to a large extent a product of (great) engineering.

In Figure 1, A, there is a cartoon of the robot, side by side with its CAD (computer-aided design) model (panel B) and the basic kinematic structure (joints and links) (panel C). Complete knowledge of the robot structure can be used to obtain a mathematical description of the robot’s kinematics. This essentially corresponds to a sequence of coordinate transformations between all the reference frames in Figure 1, D. Every such transformation consists of three translations and three rotations and has thus six degrees of freedom. However, as the robot structure is subject to specific
constraints in 3D space, four parameters suffice to characterize the transformation between
consecutive links/joints. This is the essence of the Denavit-Hartenberg convention in which every link
$i$ (imagine getting from the elbow to the wrist along the forearm, for example) is described by 4
parameters: 2 lengths, $a_i$ and $d_i$, and two angles, $\alpha_i$ and $\omega_i$. In the iCub—and in most robots for that
matter—all joints are revolute and have a single rotation axis, i.e. a single rotational Degree of
Freedom (DoF), like the human elbow (a “hinge joint”). Figure 2 shows a schematics of this
representation for the upper body of the robot.

| Link(i) | $a(i)$ [mm] | $d(i)$ [mm] | $\alpha$ [rad] | $\omega$ [rad] |
|--------|-------------|-------------|----------------|--------------|
| 1      | 2.31        | 193.3       | $-\pi/2$       | $\pi/4$      |
| 2      | 33          | 0           | $\pi/2$        | $\pi/4$      |
| 3      | 0           | 1           | $-\pi/2$       | $\pi/4$      |
| 4      | -54         | -82.5       | $-\pi/2$       | $\pi/4$      |
| 5      | 0           | -34         | $-\pi/2$       | 0            |
| 6      | 0           | 0           | $\pi/2$        | $-\pi/4$     |

TABLE I

| Link(i) | $a(i)$ [mm] | $d(i)$ [mm] | $\alpha$ [rad] | $\omega$ [rad] |
|--------|-------------|-------------|----------------|--------------|
| 1      | 23.36       | 143.3       | $\pi/2$        | 105 $\pi/180$|
| 2      | 0           | 107.74      | $-\pi/2$       | $\pi/2$      |
| 3      | 0           | 0           | $\pi/2$        | $-\pi/2$     |
| 4      | 15          | 152.28      | $-\pi/2$       | 75 $\pi/180$ |
| 5      | -15         | 0           | $\pi/2$        | 0            |
| 6      | 0           | 137.3       | $\pi/2$        | $-\pi/2$     |
| 7      | 0           | 0           | $\pi/2$        | 0            |
| 8      | 62.5        | -16         | 0              | 0            |

TABLE II

Figure 2. iCub kinematic model – upper body. (left) Matlab visualization of the kinematic chains and reference frames.
(right) Denavit-Hartenberg parameters for the head and left eye and left arm. Correspondences for certain link lengths are
marked.

**Forward kinematics and inverse kinematics.** The robot model describes the fixed characteristics of
the robot body (long-term of “offline” body representation – see later). The model in Figure 2 can be
transformed into equations, whereby the coordinate transformation needed to get from one link to
the next (e.g., from elbow to wrist) can be obtained as a simple matrix multiplication. To go over
more links/joints (e.g., from torso to hand), these multiplications are simply sequenced. In the
canonical form, this will only work for a single posture of the robot, like the one in Figure 1. To know
where the body currently is in space, it has to be combined with the robot “proprioception”: the
joint angle values. These are plugged into the equations as one of the orientation parameters ($\omega$).
This operation—combining current joint angle values with the robot model—is known as forward
kinematics, which provides a mapping from joint space to Cartesian space (also called operational
space or task space). Thus, transformations between, say, hand frame, body frame, or eye frame can
be readily obtained.
For a robot to reach to a specific position and with a specific orientation in Cartesian space—no matter in which reference frame the target is expressed as it can be transformed to the base frame—an inverse mapping is needed: from Cartesian space to joint space, i.e. to acquire the joint angles of the robot arm when the end effector (the hand) contacts the target. This is dealt with by inverse kinematics. Unlike forward kinematics, this is a harder problem and not just a matter of substituting for current joint angle values into the equations. Reaching for a target in 3D with a specific orientation constraints the robot pose in 6 dimensions (3 positions and 3 orientations). Hence, a minimum of 6 DoF—6 joints—is required on the robot part. For 6 DoF manipulators—robot arms with 6 rotational joints—that have a specific geometric structure, a closed-form solution can be obtained. That is, a solution can be found instantaneously. However, in general, one has to resort to numerical methods. Robots with more than 6 DoF have multiple ways of reaching for the target and hence are called redundant manipulators. Additional criteria are needed to choose among the solutions. In the iCub, there are 7 DoF in every arm and 3 additional ones in the torso. The manipulator is thus highly redundant. Inverse kinematics is solved numerically by using a non-linear optimizer (Pattacini, Nori, Natale, Metta, & Sandini, 2010).

Motion control. Inverse kinematics provides the joint space configuration for the robot at the final position at the target. However, it does not automatically deal with the trajectory—joint and end effector positions in time—needed to move between the initial and final position. Trajectory generation constitutes its own discipline that deals with planning such smooth movements using different interpolation methods, for example. Once the trajectory in joint space is planned, low-level motor controllers in every joint can be used to bring about the desired movements in time. In the iCub, (Pattacini, Nori, Natale, Metta, & Sandini, 2010) designed a bio-inspired dynamical systems-based controller that produces smooth, minimum jerk trajectories in which the end effector (the hand) follows a quasi-straight line.

Dynamics. While kinematics deals with positions, velocities, and accelerations, dynamics deals with equations of motion and forces that are needed to produce a particular movement. The reader is referred to any robotics textbook on the topic. For the iCub, (Nori, et al., 2015) provide an example.

3 Characteristics of body representations
In this section I will attempt to compare the most important features of body representations in animals, humans, and robots. First a note on terminology is in order. I use “body representations” as a general concept that should encompass both body schema and body image and possibly other body-related notions. However, by using the word “representation” it is not my goal to take a stance in the philosophical debate on representationalist vs. sensorimotor approaches to body awareness (De Vignemont F., 2015). The account will admittedly be biased toward the “representationalist” viewpoint (e.g., (Carruthers, 2008), (Longo, Azanon, & Haggard, 2010))—also because I come from robotics and computer science—and will not address the phenomenological perspective and the “lived body” (Merleau-Ponty, 1945). At the same time, I also fully endorse the “sensorimotor approach” and I want to avoid, or at least reflect upon, imposing the representationalist stance typical of robotics and (Good Old-Fashioned) artificial intelligence (Haugeland, 1985) onto the biological “body in the brain” (see also our attempt in (Hoffmann, et al., 2017)). (Webb, 2006) provides a useful clarification of the terms transformation, encoding, and representation. The word
representation should be reserved to the strong notion of standing in for something: properties or states of the body that can be manipulated also when the body itself cannot be used or sensed directly. Sometimes, the body can be used directly—imagine the reaching in octopus discussed above—and it is probably more natural to think that the “brain is in the body” and does not have to have it all represented, rather than that the “body in the brain” is embodied (cf. a discussion in (Alsmith & De Vignemont, 2012)).

According to (De Vignemont F., 2015), there are three principal taxonomies of body representations. I will list them below, together with their relationship to the account in this book section:

1. The triadic taxonomy based on “format” of body representations (Schwoebel & Coslett, 2005) distinguishes:
   a. sensorimotor body representation (a.k.a. body schema)
   b. visuospatial body representation (or body structural description)
   c. conceptual body representation (or body semantics)

   My account will span roughly the first two, leaving the conceptual body representation aside.

2. The functional dyadic taxonomy (Dijkerman & De Haan, 2007) (Gallagher, 2006) (Paillard, 1999), based on the perception-action model of vision (“ventral stream” or “what” vs. “dorsal stream” or “where/how” (Milner & Goodale, 2006)), distinguishes:
   a. Body schema – sensorimotor representations of the body used for action planning and control.
   b. Body image – lacking a unifying positive definition (Berlucchi & Aglioti, 2010) (De Vignemont F., 2010), comprises all the “other” (than body schema) representations about the body that are not used for action: perceptual, conceptual or emotional.

   My account will focus on the representations for action. Robot body models are also primarily geared toward action. However, interestingly, as their models are engineered from the outside, they do carry a lot of the flavor that is typical rather of the “what” pathways that care about semantics of objects etc.

3. The temporal dyadic taxonomy (Carruthers, 2008) is based on the dynamics of body representations and contrasts:
   a. long-term or “offline” body representations, such as limb size—what the body is usually like. These are relatively stable in adulthood and may include some innate components about body structure (e.g., 2 arms and 2 legs). (Carruthers, 2008) also argues “that the offline body representation must be an integrated representation, a failure to integrate leads to body integrity identity disorder.” “That is, it must represent the body as a single thing, rather than a collection of parts.”
   b. short-term or “online” representations of the body as it is currently, such as in which posture, constantly updated on the basis of afferent and efferent information.

In this case, both are obviously equally relevant. From the robotics perspective, the long-term body representation can be equated with body model. The short-term representation would be the body state. I will focus more on the long-term body representations.
To give the discussion concrete contours, let us look at the example in Figure 3: reaching to the body. Top panel (A) depicts a scenario from a series of studies on infants where they were observed reaching for a vibrotactile stimulus (buzzer) (Hoffmann, et al., 2017) (Leed, Chinn, & Lockman, 2019). Two components seem necessary: (1) localizing the stimulus on the body and (2) reaching for it. Panel A, center, depicts a possible decomposition into blocks. The left part (inside dashed area), adapted from (Longo, Azanon, & Haggard, 2010) (Tamè, Azañón, & Longo, 2019) deals with the “localization” or somatoperceptual processing part. Once the target is localized (spatial localization of touch block), it can be adopted as the reaching target (illustrated with a “~”), and the motor action can be prepared and executed. The different shapes for the blocks in the dashed area were reproduced after (Longo, Azanon, & Haggard, 2010) as follows: “inputs are depicted as diamond shapes, body representations as ovals, and perceptual processes as rectangles”. It is interesting to look at this from the temporal taxonomy perspective: it seems that only the long-term or offline modules count as representations here. The percepts, however, represent “states of the body” and can be viewed as short-term or online body representations. (Heed, Buchholz, Engel, & Röder, 2015) offer a different conceptualization of this scenario also known as tactile remapping—the transformation of a coordinate in a skin-based reference frame into a coordinate in an external reference frame by integration of posture information. Heed et al. actually present three variants of the schematics (not reproduced here): (a) remapping view, (b) integration view, and (c) sensorimotor contingency view. In (b) and (c), the arrows between the “localization” part and the “action” part point in both directions, which points to another important aspect of the problem: a sequential processing view and decoupling of the perception and action part may not be justified—something we touched upon in section Body in the primate brain. Analysis of the infant reaching behavior in the buzzer experiments shows that looking at the target and reaching often happens simultaneously; in addition, for targets on arms/hands, both the limb with the target and the reaching contralateral arm often move simultaneously (Chinn, Hoffmann, Leed, & Lockman, 2019). The more general point of recurrent connections also relates to the state estimation problem: the “percepts” may not be a result of a single pass that combines information from different sources, but may a result of conflict reconciliation where activations need to flow back and forth.
Figure 3. Reaching to the body. (A) Scenario with reaching for vibrotactile stimuli in infants (Hoffmann, et al., 2017). Photos show an infant presented with the stimulus (left), in the process of reaching (top right) and in the final posture (bottom right). Center: A conceptual model of somatosensory processing—inside dashed area—adapted from (Tamè, Azañón, & Longo, 2019) (Longo, Azanon, & Haggard, 2010), with additional blocks illustrating the motor part. (B) Schematic illustration of cortical areas that may be responsible for bringing about the behavior. (C) Similar scenario on the iCub humanoid robot: tactile stimulus (left), motor action (top right) and final configuration (bottom right). Center: block diagram illustrating the modules used to generate the “self-touch” behavior. (Roncone, Hoffmann, Pattacini, & Metta, 2014)

Credit: Brain image source (without additional legend on top): Hugh Guiney/ Attribution-ShareAlike 3.0 Unported (CC BY-SA 3.0).

Panel B schematically illustrates some of the cortical areas of monkey brain that may be involved in generating this behavior. Finally, panel C shows an instantiation of a similar scenario on the iCub humanoid robot. There is one important difference: this not a conceptualization of the behavior; this is an actual pipeline that has been used in (Roncone, Hoffmann, Pattacini, & Metta, 2014) (video: https://youtu.be/pfse424t5mQ). The blocks correspond to actual pieces of software. Surprisingly, there is quite a good match with the schematics of panel A, which may be because the schematics of Longo and colleagues is somewhat classical and thus compatible with engineering models that—mostly for practical reasons—typically follow modular design and “sense-think-act” logic.

There are almost countless characteristics of body representations that we can think of. In what follows, I will sketch some of the important ones, focusing in particular on those where contrasting the biological and robot world can bring the most insight. Hence, I will, for example, leave the unconscious vs. conscious aspect aside—as discussed above, the focus here is on the sensorimotor level. I will take a number of examples from biology and robotics, developing the ideas in (Hoffmann,
et al., 2010) (Hoffmann & Pfeifer, Robots as powerful allies for the study of embodied cognition from the bottom up, 2018). I will also, sometimes quite speculatively, attempt to chart the body schema and body image onto the hypothetical axes. Body image will largely stand for visuospatial representation of the body or body structural description—body percept rather than body concept. The brain areas involved are also only schematically illustrated.

In Figure 4, the iCub humanoid robot and the kinematic model of its upper body is depicted in panel A. The model has been essentially hand-crafted by following the Denavit-Hartenberg convention and supplying the corresponding lengths and angles from the CAD model of the robot. Panel B adds the possibility to calibrate the same model automatically as the robot exploits self-observation and self-touch configurations (Stepanova, Pajdla, & Hoffmann, 2019). Panels D and E depict other examples of robot self-calibration. (Bongard, Zykov, & Lipson, 2006) used a quadrupedal machine continuously “self-modeling” itself. The robot model had a special nature: it consisted of a physics-based simulator with a copy of the robot’s limbs, motors, sensors and even the environment. Within this, engineered, “world and body model”, the robot would search for its kinematic structure by comparing the actions and their sensory consequences from the physical world with those in the simulator. (Sturm, Plagemann, & Burgard, 2009) had a robot arm observe “itself” using a camera and infer its model—learning the structure of a Bayesian network—from motor actions and observations in the camera. Panel C schematically illustrates humans and the body schema and body image.

Figure 4. Body representation characteristics I: plasticity and number of modalities. (A) iCub humanoid robot and its kinematic model. (B) iCub kinematic self-calibration using self-observation and self-touch (Stepanova, Pajdla, & Hoffmann, 2019). (C) Human and schematic illustration of brain areas important for body representations: body schema (see Figure 3 for details) and body image (Posterior Parietal Cortex (PPC), Extrastriate Body Area (EBA), Insula – after (Berlucchi & Aglioti, 2010)). (D) Four-legged machine learning its body structure (Bongard, Zykov, & Lipson, 2006). (E) Robot manipulator learning body structure from self-observation (Sturm, Plagemann, & Burgard, 2009). Figure revised and expanded from (Hoffmann & Pfeifer, Robots as powerful allies for the study of embodied cognition from the bottom up, 2018).

Credit: A - iCub cartoon: Laura Taverna, Italian Institute of Technology. Credit: C – Walking human: Public domain (https://commons.wikimedia.org/wiki/File:BSicon_WALK.svg). Credit: Body schema brain image source: Hugh Guiney/ Attribution- ShareAlike 3.0 Unported (CC BY- SA 3.0). Credit: Body image brain image source: Public domain
Plasticity. Let us first consider plasticity or adaptivity of body models. Traditional robot models are fixed: an industrial manipulator is shipped with its model. It may not be directly available to the customer, but it will be embedded in the robot controller which needs the robot model(s) for operation. Even industrial robots may require occasional (re-)calibration, which can be performed using different routines. Less accurate or more complex robots, such as humanoids, may need recalibration more frequently. The work (Stepanova, Pajdla, & Hoffmann, 2019) (Figure 1, B) is one of many examples in which the robot kinematic model parameters are calibrated. The approach is rather straightforward: redundant information about positions of certain body parts—from self-touch or self-observation in this case—drives learning: with two hands physically touching and both cameras observing the point, any mismatch between the position of the corresponding point —after remapping into a common frame of reference—generates an error term used to update the model (all but the grey parameters are calibrated). Body representations in primate brains (panel C) are known for their plasticity on several time scales: first, body models need to be discovered by the brain, starting already in the fetal period (see the work of Kuniyoshi and colleagues on embodied computational models of this – Section 4). Second, body models need to adapt, as the body grows for example. Third, they adapt or optimize when some body parts are frequently used in a specific task—when playing a musical instrument, for example. Fourth, they adapt also on very short time scales like when adapting to tools or when the subject is tricked by some of the numerous illusions, like the Pinocchio illusion. In the last case, it is rather a case of “short-term body schema” adaptation—a state estimation process—rather than adaptation of the body model itself, although this may be happening simultaneously and some after-effects observed. Next to the temporal taxonomy (online vs. offline body representations), I will speculate about the distinction between body schema and body image on the plasticity axis. It seems that most of the rapid recalibrations pertain to the body schema which draws more directly on the inputs from different modalities and their integration. Taking the Rubber Hand Illusion (Botvinick & Cohen, 1998) as an example, the body schema adaptation is manifested in the proprioceptive drift; however, the participants also start to quickly incorporate the rubber hand into their bodies—“own” the rubber hand—which is typically associated with body image (and the insula). The suggested primacy of body schema over body image (Pitron, Alsmith, & de Vignemont, 2018) may also be relevant here: body schema adaptation may, in a second step, propagate to body image.

It seems that the brain is rather “liberal” about the constraints imposed on the models and can be led into believing highly improbable things, like the “nose elongation” during Pinocchio illusion. Robot models, on the other hand, tend to have quite strict constraints or bounds on the model parameters—capitalizing on the knowledge available from the outside—and would thus not fall for the illusions easily. At the same time, there are limits to the plasticity. Important evidence suggestive of innate and fixed—immune to experience—components of body models comes from the phantom limb phenomenon, which may be experienced following amputation but even in some subjects who congenitally lack limbs (e.g., (Ramachandran & Blakeslee, 1998)). That is, the basic body layout may be to some extent hard-wired in the model and immutable. The self-calibrating robots D, E in Figure 4 move in that sense beyond this as they are able to learn any topology of their body layout—that is why they are positioned more to the right on the plasticity axis. However, this is clearly an oversimplification: these robots surpass the brain plasticity in this single aspect only.
Multimodal nature of body models. Standard robot models are amodal—they do not depend on any sensory modality; they directly describe physical reality like the geometry of the body—see Figure 2 or Figure 4, A. This holds in some sense also for all the other robot body models in Figure 4: B, D, E. In B, the robot model itself is identical to that of A. The sensory modalities—proprioception, touch, and vision in this case—are needed to collect the redundant information about the body’s position in space and update the model. This layer is separated from the model of the robot geometry itself. In D, E, the situation is quite similar. Similarly to B, E features self-observation. In D (Bongard, Zykov, & Lipson, 2006), three modalities—touch, tilt and clearance—are used to compare their values from the real robot with those from alternative body layouts in the simulator. Based on this, the case studies are localized on the “modality” axis. Body representations in the brain are famous for their “multimodality” (Azañón, et al., 2016) review the multisensory contribution to body representations: visual, somatosensory (tactile and proprioceptive), vestibular, auditory, and nociceptive. Hence, “body in the brain” scores highest on the “multimodality axis” in Figure 4. A divide-and-conquer approach is used throughout the article by Azañón et al.—modality by modality. This is also discussed by the authors: such an approach is useful experimentally, but implausible in reality as there would be a lot of “cross-talk” between the modalities. Indeed, the body representations are assumed to be in some sense unified or coherent. In light of the works in robot self-calibration, this begs the question whether the brain arrives in some sense to an amodal, modality-independent, model of the, say, body in space, onto which different sensory modalities converge. This resembles the emulation theory of representation proposed by (Grush, 2004) who uses the Kalman filter metaphor: the amodal, long-term body model is a central representation, which also includes its relationship with individual sensory modalities. The filter can then perform state estimation—current state of the body—by performing a “sensory update”. To what extent this would be the case for the brain remains unclear. Different distortions of body perception—inhaling some properties of the imperfect representations of individual modalities like the somatosensory homunculus—seem to suggest that the brain has not synthesized a perfect amodal model of its body (see e.g., (Fuentes, Longo, & Haggard, 2013) (Longo M. R., 2015)). Finally, we can probably say that the body schema is more strongly multimodal, while the body image—at least as a pictorial description of the body based on a mainly visual exteroception—would be less multimodal.

Explicit/veridical vs. implicit/embodied body models. Robot body models are explicit: it is clear what in the model corresponds to what in the body (e.g., a certain parameter to the length of the left forearm—see Figure 2 and Figure 5 A). They are also objective and veridical: the parameters should be the true physical values of the quantities (lengths, angles, masses, etc.). In the biological realm, representations in general are not like that. Of course, this depends on the school of cognitive

2 Coming from signal processing, a Kalman filter is an efficient recursive filter—device or process that removes some unwanted components or features from a signal—that estimates the internal state of a linear dynamic system from a series of noisy measurements.

3 Grush, taking human arm as an example, contrasts an internal model in the form of a look-up table storing previous input-output sequences with an articulated model—a model that includes some variables corresponding to their counterparts in the musculoskeletal system (e.g. elbow angle, arm angular inertia, tension on quadriceps). Some of these variables can be measured (e.g., by stretch receptors) and these sensors can also be simulated in the emulator.
science, but there seems to be growing consensus about the embodied and action-oriented nature of cognition (e.g., (Engel, Maye, Kurthen, & König, 2013)). This should hold for representations of the body as well (Alsmith & De Vignemont, 2012). “What the nervous system needs to do, in general, is to transform the input into the right action.” (Webb, 2006) We can take again the example of reaching behavior. As discussed above (The invertebrate brain and reaching in octopus), the octopus is able to reach for visual targets, but it may not know—and may not need to know—how long its arm is or where it is exactly in space. Orienting the base of the arm and propagating the bend until contact is detected by the suckers may well suffice. This is embodied action and may be in line with the fact that no specific body representation—somatotopic or other—sites were found in its nervous system. The need to represent the body, its state, and the complex inverse kinematics and dynamics, has been largely offloaded to embodiment: the properties of the muscular hydrostat, supported by the peripheral nervous system and low-dimensional inputs from the central nervous system. This is also in line with the thinking of (Cisek & Kalaska, 2003) who highlight the importance of the online, dynamically generated, character of movement generation. At the same time, they also point out that due to conduction delays inherent in the sensorimotor system, purely feedback control is limited, or at least slow (perhaps manifested in the octopus experiments of (Gutnick, Byrne, Hochner, & Kuba, 2011)). Successful action is also the only criterion for the “quality” of what is represented about the animal’s body in its brain: there is no need for any objective or veridical representation. Hence, the octopus has been positioned on the far right of the x-axis in Figure 5. Insects would be even farther right on this axis, with their “body in the nervous system” so implicit that that we may be reluctant to call this representation altogether.

Figure 5. Body representation characteristics II: explicit vs. implicit and serial vs. parallel. (A) iCub humanoid robot and its kinematic model. (B) iCub learning to reach using deep learning (Nguyen, Hoffmann, Pattacini, & Metta, 2019). (C) Human and schematic illustration of brain areas important for body representations: body schema (see Figure 3 for details) and body image (Posterior Parietal Cortex (PPC), Extrastriate Body Area (EBA), Insula – after (Berlucchi & Aglioti, 2010)). (D) Octopus and schematic of its nervous system.

Credit: A - iCub cartoon: Laura Taverna, Italian Institute of Technology. Credit: C – Walking human: Public domain (https://commons.wikimedia.org/wiki/File:BSicon_WALK.svg). Credit: Body schema brain image source: Hugh Guiney/
Similar arguments hold for primate brains but to a lesser extent. Numerous sites dedicated to representing the body were found (Figure 3, B; Figure 5, C). For reaching, some evidence is suggesting that common reference frames encoded in neurons in the posterior parietal cortex may be used for movement plans (Cohen & Andersen, 2002), for example. However, “neurophysiological studies routinely fail to find a significant population of cells whose activity explicitly encodes the output of that transformation in a unique coordinate system. Instead the output may be implicitly embedded in the distributed pattern of activity across the population…” (Cisek & Kalaska, 2003); see also (Heed, Buchholz, Engel, & Röder, 2015). This is perhaps even more prominent in the motor cortex, where it is still being debated what it is the cells are specifying about reach: muscle force, movement direction, or a more abstract end goal of muscle action (Lisman, 2015). Somatotopy is rather functional than based on the spatial relationships of the body. The embodied perspective is also appropriate here—see (Corbetta, Wiener, Thurman, & McMahon, 2018), for example. At the same time, compared to the octopus, much more of the body seems more explicitly represented. Interestingly, (Longo M. R., 2015) also considers the implicit-explicit axis for body representations and draws a line roughly between the “body schema” and the “body image”. In tasks more related to action and where humans do not consciously represent their body, the body models seem more implicit and also less accurate. These representations may also be dominated by somatosensation and inherit some of the distortions typical of the “somatosensory homunculi”. Conversely, tasks that relate to conscious perception of our body seem to draw on more explicit representations that are also more accurate/veridical (e.g., image of our hand). This is schematically illustrated in Figure 5, C.

Finally, works in robotics can also move toward more implicit models—this is in line with the current advent of deep learning and end-to-end architectures. One example on the iCub robot is in Figure 5, B (Nguyen, Hoffmann, Pattacini, & Metta, 2019). From motor babbling experience, the robot learns to associate the head and eye configuration and stereo-image input with arm joint configuration required to reach, together with the body part that will contact the object. The complete mapping is implicitly represented in a deep convolutional neural network. Only the feedforward component is represented, not the motor execution, which is performed using traditional methods.

Serial vs. parallel processing. Another axis that separates robot body models from their biological counterparts is serial/sequential vs. parallel processing (y-axis in Figure 5). This has to do with the design but also with the computing substrate. Robot control architectures tend to have a serial “sense-think-act” design; in addition, their control systems run on substrates derived from the classical von Neumann architecture. Biological brains are known for their massively parallel processing. This is nicely illustrated on the example of visually guided behavior in Figure 6 from (Cisek & Kalaska, 2003). Interestingly, (Pitron, Alsmith, & de Vignemont, 2018) suggest some serial aspect of body representations whereby the body schema would be feeding the body image.
Figure 6. Sequential vs. parallel processing for visually-guided behavior. (A) The traditional “sequential processing” model of visually-guided behavior. In this model, visual input is used to construct a model of the world which is used to make decisions. After decisions are made, a desired trajectory is generated and executed. (B) Schematic representation of the “specification and selection” architecture for visually-guided behavior. Under this view, visual information has two different roles: specifying the parameters of potential motor actions; and defining criteria which bias competition among those potential actions until a single action is selected. These biasing factors include attention, behavioral relevance, prior reinforcement, required effort, behavioral context, learned associations, motivations, long-term behavioral objectives, desired outcomes, and any other factor which influences action selection. The processes of specification and selection occur in parallel, and continue even during overt movement. A striking feature of this architecture is the absence of a central model of the visual world. Figure redrawn and caption from (Cisek & Kalaska, 2003).

A second aspect is the presence of recurrent connections. In robot control systems, the flow of information is sequential and also unidirectional. Conversely, in neural systems, recurrent connections are ubiquitous. In primate brains, due to their complexity, hierarchies are formed and information flows back and forth, combining the bottom-up and top-down influences at different stages of the hierarchy. This is valid universally, circuitry responsible for representing the body not being an exception. The recurrent nature is also more pronounced in primate nervous systems than in cephalopods, say—mainly due to the overall difference in the number of neurons and layers of processing. This difference has also implications on the nature of the online, or short-term, body representations. In traditional robot frameworks, state estimation will be at the top of the sensory processing part, perhaps combined with priors from the model. However, in the brain, state estimation is a highly dynamic, continuous process combining multisensory integration, top-down priors etc.—through recurrent loops. Finally, the robot case study (Figure 5, B) features a purely feedforward, hence sequential, neural network.

Modular vs. holistic and centralized vs. distributed representations. A final graphical attempt to contrast body models in robots and animals is depicted in Figure 7. At first glance, it would seem intuitive that robot models are centralized, while “body in the brain” highly distributed. There is typically only one body model for a robot. In contrast, in the brain, there are numerous distributed, incomplete, body representations. In this sense, there is some overlap between centralized vs. distributed and the explicit vs. implicit distinction. However, centralized in this case does not imply monolithic. In fact, robot body models and associated control modules are highly modular—as shown in Figure 7 A. There are distinct modules like forward/inverse kinematics and dynamics that
may draw from the same robot model and be recruited for different purposes like state estimation, movement planning etc. There would be typically only one module of every kind (imagine a software library) providing this functionality upon request. The representations/modules will thus be universal (as opposed to task-specific) and not overlapping. In nervous systems, on the other hand, there would be often complete sensorimotor loops specialized on a particular task (and hence task-specific rather than universal). In that sense, every such representation would be in some sense holistic. Their functionality may also be partially overlapping or redundant. Population coding is a good example: it is striking how unspecific the receptive fields of individual neurons often are (e.g., (Georgopoulos, Kalaska, Caminiti, & Massey, 1982)). Also, many tasks may require some form of representation of hand in space, say, but it cannot be excluded that this will be implicitly “implemented” multiple times. This distributed, specialized, and holistic nature is highest for the octopus nervous system (Figure 7, C); regarding body models in primates (Figure 7, B), the body schema as evolutionarily older and more “low-level” is on these axes expected closer to octopus, whereas the body image somewhat closer to the engineered body models.

Figure 7. Body representation characteristics III: modular vs. holistic and centralized vs. distributed. (A) iCub humanoid robot, its kinematic model and some control modules. (B) Human and schematic illustration of brain areas important for body representations: body schema (see Figure 3 for details) and body image (Posterior Parietal Cortex (PPC), Extrastriate Body Area (EBA), Insula – after (Berlucchi & Aglioti, 2010)). (C) Octopus and its nervous system.

Credit: A - iCub cartoon: Laura Taverna, Italian Institute of Technology. Credit: B – Walking human: Public domain (https://commons.wikimedia.org/wiki/File:BSicon_WALK.svg). Credit: Body schema brain image source: Hugh Guiney/ Attribution-ShareAlike 3.0 Unported (CC BY-SA 3.0). Credit: Body image brain image source: Public domain (https://commons.wikimedia.org/wiki/File:Gray731.png). C - Common octopus - albertkok / CC BY-SA (https://creativecommons.org/licenses/by-sa/3.0). D - Octopus nervous system - Jean-Pierre Bellier / CC BY-SA (https://creativecommons.org/licenses/by-sa/4.0).
4 Robots as embodied models of body representations

How can the biological disciplines like cognitive psychology and neuroscience profit from the viewpoint of robot models? The engineering perspective provides mature analytical machinery that deals with the relevant problems and this can be certainly exploited. For example, consider again the “multimodal nature of body models” discussed above. Next to the Kalman filter metaphor employed by (Grush, 2004) to describe how estimating the current body state might work, mathematical methods can be also employed to answer fundamental questions like under what exact conditions can an agent (or “the brain”) discover the (amodal) notion of space in which it is embedded and infer its dimensionality from sensorimotor flow only. According to (Piaget, 1954), for the infant, initially, “no constant relation exists between visual and buccal space or between tactile and visual space. True, auditory and visual space are already coordinated, as are buccal and tactile space, but no total and abstract space encompasses all the others.” Later, these spaces are connected through prehension (reaching and grasping), the “near” and “far” space become differentiated. Eventually, through “reversible operations”—for example, whether the object moves in front of me or I move the head, the image on the retina will be the same—the child may overcome the space of individual modalities and “objectify” the world, space, and its body: the body, say, will appear as an object with certain dimensions, independent of its perception by individual senses. Mathematical and algebraic tools and robotics can formalize Piaget’s ideas and provide existence proofs under what exact conditions may an agent develop spatial knowledge and give precise content to these concepts. Pioneered by Henri Poincaré, compensability (“ reversible operations) was exploited by (Philipona, O'Regan, & Nadal, 2003) who showed how an agent can infer the dimensionality of space from proprioception and exteroception and this was extended by (Terekhov & O'Regan, 2016) to use coincidence detection in neural networks as the basis of a way of discovering the notion of space. (Laflaquière, O'Regan, Argentieri, Gas, & Terekhov, 2015) explicitly considered the agent’s “point of view” in the sensorimotor flows. An alternative approach makes use of self-contact: the “body in space” can emerge from the structure of the proprioceptive-tactile space in self-touch configurations (Roschin, Frolov, Burnod, & Maier, 2011) (Marcel, Argentieri, & Gas, 2016). Such models do not prove that these solutions are used by the brain, but they provide hypotheses and one can then look for them in the neural code.

Second, next to models at a high level abstraction like the simulated sensorimotor agents, robotics can provide a much higher degree of realism when it comes to mimicking biological bodies. This may be necessary to make progress beyond the existing models addressing coordinate transformations or multisensory integration (Xing & Andersen, 2000) (Pouget, Deneve, & Duhamel, 2002) that typically concern very simplified scenarios with 1D or 2D geometry, one or two joint angles for the proprioceptive modality, etc. More than 15 years of research in the lab of Yasuo Kuniyoshi stands out in this respect: a highly realistic musculo-skeletal fetal simulator (21 rigid body parts connected by 20 joints with 36 degrees of freedom, 390 muscles with proprioceptive receptors and 3,000 tactile mechanoreceptor models) has been developed and coupled to a spinal circuit model (neural oscillators, α and γ motor neurons, and sensory interneurons) and a cortical model (2.6 million spiking neurons and 5.3 billion synaptic connections) (Yamada, et al., 2016). Figure 8, (A), shows the human-like distribution of tactile receptors on the fetus body. (Mori & Kuniyoshi, 2010) studied the effect of this distribution on the emergence of sensorimotor behaviors: with a natural (nonhomogeneous) distribution, the fetus developed ‘normal’ kicking and jerking movements (i.e.,
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similar to those observed in a human fetus), whereas with a homogeneous allocation it did not develop any of these behaviors—just one illustration of the importance of the need for embodying the models related to body representations. Simulating physics can be computationally heavy and there is always a risk that the simulator does not get certain properties right. Therefore, physical robots are an indispensable tool. Figure 8 (B) shows one of a series musculo-skeletal humanoids: Kenshiro (160 "muscles"—50 in the legs, 76 in the trunk, 12 in the shoulder, and 22 in the neck) (Asano, Okada, & Inaba, 2019). Such platforms provide the right challenge to model the impact of the details of the motor system on body representations and reaching behaviors. (Richter, et al., 2016) have combined a musculoskeletal robotics toolkit (Myorobotics) with a scalable neuromorphic computing platform (SpiNNaker) and demonstrated control of a musculoskeletal joint with a simulated cerebellum. Finally, the iCub baby humanoid robot (Figure 8 (C)) is my platform of choice for models of body representations. It lacks some of the biological detail of the other platforms—its whole-body skin has a uniform density of tactile receptors and it is driven by standard electric motors rather than artificial muscles—but it is a very versatile platform with all the key sensory and motor capacities. For example, we showed how it can be used to learn its “somatosensory homunculus” (Hoffmann, Straka, Farkaš, Vavrečka, & Metta, 2018) or self-calibrate using self-touch (Roncone, Hoffmann, Pattacini, & Metta, 2014) or self-touch and self-observation (Stepanova, Pajdla, & Hoffmann, 2019).

5 Which characteristics of biological body representations should robots take on board?

What properties that biological body representations manifest should robot models copy? One feature that is clearly desirable is adaptivity. Robot models need to be developed in the first place. Then, additional calibration procedures may be required for every robot exemplar and also after
deployment on the factory shop floor. During operation, the robot is subject to wear and tear or other conditions might change, calling for additional calibration. All of these processes are costly and often require the intervention of professionals with specialized equipment and possibly suspending production. The “body in the brain”, on the other hand, seems to develop largely from scratch and displays plasticity on all of these time scales: adapting to growth or failures as well as performing rapid recalibration when working with a tool, for example. Automatic robot self-calibration is thus desired and solutions for this are being developed. For the robot to self-calibrate, it needs redundant sources of information about its body. There is a growing number of powerful yet economic sensors for robots available (cameras, RGB-D cameras, inertial measurement units, force/torque sensors, tactile sensors) and they can be exploited for calibration. Multimodality—another property of biological body representations—thus enables plasticity (see Figure 4). Such an extension of robot models should thus be unproblematic and is already happening.

I have sketched also other axes: robot body models are typically explicit, veridical (Figure 5), universal, centralized, and modular (Figure 7). All of these are—from an engineering perspective—very convenient properties. For example, being explicit and universal often implies that the models are capable of extrapolation: if transformations in 3D space are represented using appropriate mathematical tools, they will always work—even in previously unseen circumstances. Implicit models would typically be expected to interpolate only, i.e. provide meaningful estimations within the range of existing examples only. Being veridical, or objective, implies that robot body models can be easily validated from the outside. The universal, centralized, and modular nature is ideal from a maintenance perspective. The kinematic model is only in one place and any updates will be automatically propagated to all other modules using it. One important additional convenient property that is a consequence of the features listed above is interpretability: it is possible to understand the model which is key for maintenance, debugging etc. In this sense, there seem to be good reasons for preserving these properties.

Yet, these very characteristics are responsible for some inherent limitations. In particular, robot body models and associated control architectures lack robustness. The centralized and universal feature makes every module critical and that creates bottlenecks. Redundancy is against software development principles, but it importantly contributes to the resilience of animals. When faced with injuries, impairments, or lesions, they can find alternatives to performing a task. Implicit models are gaining popularity with the advent of deep learning—see (Nguyen, Hoffmann, Pattacini, & Metta, 2019); for a survey in robotics, see e.g., (Sünderhauf, et al., 2018). This can be seen as a step toward brain-like models. Making robot control more embodied—exploiting the body morphology or local feedback loops—would be another step in this direction. However, there are trade-offs associated with this: mainly, the interpretability of such implicit, or black-box, models is reduced, which is a downside when they are part of applications where for example safety is at stake. Another difference is the sequential vs. parallel processing (Figure 6). Having multiple potential movements plans always ready will also improve the robustness of robot behavior when faced with unexpected situations.

In summary, the strategy employed in robot modeling and control—a single, universal, veridical body model associated with corresponding control schemes—makes robots rather brittle when faced with failures or unexpected changes. Instead, the solution evolved by animals—multiple,
distributed, partially overlapping, task-specific, and parallel architectures—makes them particularly robust and resilient.

6 Discussion and conclusion

I have outlined a number of characteristics of robot body models as well as body representations in nervous systems. Most often, the nature of these models is very different, often ending up on opposite ends of different schematic axes. The seems to be a general trend: on many of the axes sketched in Section 3, the sequence is from robot body models, over body image, body schema, to the body representation in the octopus. Paraphrasing Brooks (Brooks, 1991), the octopus is most faithful to the strategy that The body is its own best model. Despite the efforts of Brooks and others, robots still heavily rely on models of their bodies—fixed, amodal, explicit, veridical, serial, centralized, and universal. Interestingly, the body image is the second closest to the robot side which begs the question—asked by Yochai Ataria—to what extent may the robots be like Ian Waterman, the famous “man who lost his body” (proprioception and touch) (Cole & Paillard, 1995). Indeed, just like deafferented subjects that “lost their body schema”, robots rarely recruit an implicit sensorimotor representation of their body or the body directly (without modeling it; see also (Hoffmann & Müller, Simple or complex bodies? Trade-offs in exploiting body morphology for control, 2017)). Also, as their body models are explicit and veridical, they resemble the “pictorial”, body image-like representation of their bodies. Vision is also the main sensory modality and most self-calibration approaches rely on it. One difference remains: robots have proprioception—joint angle readings from encoders—and these together with vision are employed to bring about reaching movements. However, they rarely have touch (and may be clumsy and slow just like Ian Waterman) and without their body model cannot do pretty much anything.

We have seen that the way animals and machines represent their bodies is quite different. Can robots contribute to our understanding of the “body in the brain”? As we have seen in Section 4, this can be the case in two ways: (i) employing the mathematical machinery can provide proofs of what is possible—extracting body as an object in 3D from multimodal sensory information, for example; (ii) using robots as embodied computational models of body representations. In all cases, one should reflect upon using robots, such that the “design decisions” typical for robot models are not blindly applied to the biological world. In terms of performance (Section 5), interestingly, the rather “messy” way adopted by biology—which is also why our understanding of the mechanisms is still limited—is surprisingly good. Neither the models nor the behavioral performance is optimal, but it is good enough and highly robust. On the other hand, robot body models and control are very neat, transparent, universal and overall highly parsimonious and optimized. Yet, the performance is fragile. One factor to consider here is that the criterion for quality of the models in animals is the success in the action/task for which the particular body representations were recruited. Robot body models ultimately also serve actions; however, the criterion for model quality is typically rather that it is a veridical representation of something—the robot link length, for example. The deep learning type of models may provide one of the ways of bridging machine learning and neuroscience (e.g., (Richards, et al., 2019)).
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