Published in final edited form as: Conscious Cogn. 2021 May 01; 91: 103117. doi:10.1016/j.concog.2021.103117.

The 'First Prior': from Co-Embodiment to Co-Homeostasis in Early Life

Anna Ciaunica^{*,1,2}, Axel Constant³, Hubert Preissl⁴, Katerina Fotopoulou⁵

¹Institute of Philosophy, University of Porto, via Panoramica s/n 4150-564, Porto Portugal

²Institute of Cognitive Neuroscience, University College London, WC1N 3AR, London, UK

³Theory and Method in Biosciences, The University of Sydney, Level 6, Charles Perkins Centre D17, Johns Hopkins Drive, NSW 2006, Australia

⁴Institute for Diabetes Research and Metabolic Diseases of the Helmholtz Center Munich at the University of Tübingen; Department of Internal Medicine IV, Division of Endocrinology, Diabetology, and Nephrology, University Hospital Tübingen; German Center for Diabetes Research (DZD e.V.), Tübingen, Germany

⁵Research Department of Clinical, Educational and Health Psychology, University College London, Gower Street, London WC1E 6BT, UK

Abstract

The idea that our perceptions in the here and now are influenced by *prior* events and experiences has recently received substantial support and attention from the proponents of the Predictive Processing (PP) and Active Inference framework in philosophy and computational neuroscience. In this paper we look at how perceptual experiences get off the ground from the outset, *in utero*. One basic yet overlooked aspect of current PP approaches is that human organisms first develop *within* another human body. Crucially, while not all humans will have the experience of being pregnant or carrying a baby, the experience of being carried and growing within another person's body is *universal*. Specifically, we focus on the development of minimal selfhood in utero as a process *co-embodiment* and *co-homeostasis*, and highlight their close relationship. We conclude with some implications on several critical questions fuelling current debates on the nature of conscious experiences, minimal self and social cognition.

Keywords

in utero perception; embodiment; homeostasis; allostasis; predictive processing; active inference; minimal self

1 Introduction

Recent years have witnessed an 'embodied turn' in examining perception, cognition and action from a situated and embodied viewpoint (Varela et al. 1991, Gallagher 2000;

^{*}Corresponding author: a.ciaunica@ucl.ac.uk.

Thompson 2007; de Jaegher & Di Paolo 2007; Chemero 2009). The idea basic idea is that our bodies' survival within a wider and potentially threatening physical and social environment lies at the core of our perceptual experiences and cognitive processes. The embodied cognition approach outlines the idea that perception and cognition are first and foremost *embodied activities* (Noë 2004; Sheets-Johnstone 2011). In this view, cognition is "the enactment of a world and a mind on the basis of a *history* of the variety of actions that a being in the world performs" (Varela et al. 1991:9, our italics).

The idea that our ongoing perceptions, cognitive processes and actions are influenced by *prior* events and experiences has recently received substantial support and attention from the proponents of the Predictive Processing (PP henceforth) and Active Inferences framework¹ (AIF henceforth) in philosophy and computational neuroscience (Friston 2005; Clark 2013; Hohwy 2013; Fotopoulou 2015). The basic starting point is the idea that humans are biological agents that "emerge as proactive survival-enabled prediction machines" (Clark 2013:1).

In order to keep track of the survival- and reproduction-relevant bodily and worldly information, the human brain generates self- and world models, by extracting statistical patterns of information from its embodied and worldly interactions (Conant & Ashby 1970). These generative models of the cause of incoming sensory inputs are based on Bayesian 'prior' beliefs² about the likely 'hidden' causes of the sensory information. These models form the basis of the so-called 'expectations' of the agent about the causal structure of its internal and external world (Rao & Ballard 1998; Friston 2005).

In a nutshell, our ongoing perceptions, cognition and actions are processed through the lens of prior self- and world-related information processing. If this is so, then it becomes crucial to look at how these perceptual inputs get off the ground from the outset.

In this paper we lay the theoretical basis for understanding how humans self-regulate their homeostatic bodily states and build their most basic self- and world-model, literally through others' bodies, *in utero*. Specifically, we define in utero development as a process co-embodiment and co-homeostasis, and highlight their close relationship.

Indeed, one basic yet overlooked aspect of current PP and AIF approaches in both philosophy and cognitive neuroscience is that brains (and minds), and human bodies, first develop *within* another human body. The most basic perceptions and actions emerge already *in utero* (Young 2005; Zoia et al. 2007; Castiello et al. 2010; Piontelli 2010; Lymer 2011; Ciaunica & Crucianelli 2019; Quintero & de Jaegher 2020). Crucially for our discussion here, while not all humans will have the experience of being pregnant or carrying a baby, the experience of *being carried and growing within another person's body* is universal³.

Previous work looked at sensorimotor, homeostatic and bodily mechanisms operating already in early stages of development (Delafield-Butt & Gangopadhyay 2013; Ciaunica

¹We use the abbreviation AIF instead of AI (Active Inference) in order to avoid potential confusion with Artificial Intelligence (AI). ²'Belief' here is defined as a probabilistic representation encoded by neuronal activity in a hierarchical Bayesian network.

³Throughout this paper we will use the terms 'pregnant person' and 'mother' interchangeably, irrespective of their self-identified gender.

Conscious Cogn. Author manuscript; available in PMC 2021 November 25.

2016; Ciaunica & Fotopoulou 2017; Fotopoulou and Tsakiris 2017; Atzil and Barrett 2017). Here we focus on pregnancy, a case where two individuating organisms literally grasp/ grip one into each other. Specifically, we stress the idea that if we endorse a developmental bottom-up perspective, then embodiment should be examined through the lens of *co-embodiment* in humans. Contrary to the common view of the foetus being passively 'contained'⁴ and solipsistically 'trapped' in the solitude of the womb, we will present evidence speaking in favour of an active and bidirectional co-regulation and constant negotiation between the two living bodies (Martinez Quintero & de Jaegher 2020), what we will call '*co-homeostasis*'.

This paper proceeds as follows. We start in Section 2 by providing a minimal working definition of 'embodiment', before introducing the key notion of co-embodiment. The co-embodiment thesis will allow us to lay the preliminary ground for introducing the notion of homeostasis, allostasis and 'co-homeostasis', in section 3, where we will propose an active inference reading of *in utero* development of perceptual experiences. We then show that the case of pregnancy offers a clear and fundamental example of co-embodiment, in section 4, building upon theoretical and empirical work tackling the emergence of perceptual experiences *in utero*. Section 5 briefly discusses potential implications of endorsing a developmental perspective on current discussions regarding the nature of the human selfhood and conscious experiences. We conclude that when it comes to understanding the nature of our perceptual experiences and embodiment, the 'infant is father to the human' - to paraphrase Wordsworth.

2 Introducing co-embodiment

A growing body of work in philosophy, psychology and neuroscience proposed that the body plays a key role in constituting and structuring our most basic sense of self (Gallagher 2000; Damasio & Damasio, 2006; Legrand, 2006; Seth et al. 2012; Limanowski & Blankenburg, 2013; Apps & Tsakiris, 2013; Blanke et al. 2015; Seth & Tsakiris 2018; Allen & Tsakiris 2018). The embodied aspects of self-related experiences have been extensively investigated in the literature (Berlucchi & Aglioti, 1997; Damasio, 1999; Panksepp, 1998; Blanke, 2012). Moreover, the relation between the body and the self gave rise to a rich palette of theoretical debates that we cannot address here in detail (Gallagher 2013; see Qin et al. 2020 for a recent review). In what follows we use the term embodiment in its minimal form to refer to the instantiation of bodily properties by a given individual (in our case, a human). All talk about embodiment can thus be conceptually and ontologically linked to talk about embodied beings and their bodily properties.

One can distinguish between *embodiment* and the *sense of embodiment* which corresponds to the associated phenomenology, including feelings of body ownership or 'mineness' (Zahavi 2005). *Body ownership* refers to the special perceptual status of one's body, which makes bodily perceptions seem unique to oneself (Gallagher 2000; Tsakiris 2010; de Vignemont 2010). Note that embodiment is a necessary condition for the feeling of body

 $^{^{4}}$ For example, Kingma (2019) identified two options for conceiving of the relation between fetus and maternal body: (i) the fetus is merely contained within the maternal body; (ii) or it is a part of the maternal body.

Conscious Cogn. Author manuscript; available in PMC 2021 November 25.

ownership: I cannot feel that E is mine without E being embodied. Here we will focus on embodiment only, and we leave the question of the associated phenomenology aside.

As we saw earlier, the key idea behind the embodied turn in understanding perception, cognition and action is that minds (and brains) do not occur in a vacuum, but they are fundamentally linked to a body situated within a given physical and social environment (for example, humans do not live underwater, and they are highly social creatures). Crucially however, human bodies do not emerge in a vacuum either. Indeed, one fundamental yet overlooked aspect of our embodiment is that the human organism emerges and develops *within* another human body. While the experience of pregnancy has been traditionally linked to a certain category of individuals (pregnant persons), here we would like to draw attention on the critical point that, to date, all humans shared their bodies with the body of another person. Consequently, one needs to adapt and extend the notion of embodiment to reflect the fundamental and universal body-within-a-body case.

What does it mean to say that two agents are co-embodied? In biological terms, it means that the regulation of the two agents states – and particularly the need to maintain physiological stability despite a fluctuating and unpredictable environment – is actively negotiated between the two organisms that share for a given amount of time (typically 9 months) common bodily and environmental resources. An example may help us grasp this point. Consider the following two cases.

- (1) Suppose E1 and E2 are performing a circus show and they need to share pair of trousers: E1 puts her left leg into the left side of the trousers whereas E2 puts her right leg into the right side. Their task is to walk together in a coordinated manner to reach a target, say. Now, suppose E1 hits his toe against a rock, stumbles and falls, experiencing thereby fear and undergoing significant increase in cortisol levels (the stress hormone). E1 may then entrain E2 in her fall, in which case we can say that their bodies are falling *together* or that they are both sharing the experience of the fear. Crucially however, there is a sense in which the subsequent rise of cortisol levels in E1's body triggered by the stressful negative event is not *necessarily* processed the same way as that in E2's. For example, E2 may show exceptional self-control and manage to keep her balance and avoid the fall altogether (tearing apart the trousers' tissue). Or E2 may not experience fear at all, but amusement, say.
- (2) Now, consider the case of a pregnant person hitting her toe against a rock and falling. Again, E1 (the mother) and E2 (the baby) are falling *together*. Crucially, in this case E2 *necessarily* falls too. There is no way in which the foetus can 'escape' or avoid this joint fall. Similarly, the cortisol levels may rise in E1 due to the experienced fear, and interoceptive information processing will be *necessarily* linked to E2's bodily self-regulatory activity. E2 cannot actively escape it or ignore it, and her own bodily processes are directly and intrinsically impacted by E1's bodily processes (e.g. cortisol level, heart rate acceleration, oxygen level, etc.). It is important thus to distinguish the case of pregnancy from cases where two bodies contingently happen to share a state.

The key idea here is that E1 and E2 are co-embodied and strongly coupled together within the boundaries of a shared organismic state: the pregnant state. Call this *the co-embodiment thesis*⁵. Two (or more) organisms are co-embodied in this strong sense if they are bound to share bodily and environmental resources for a set time period (typically 9 months) for survival purposes. The fascinating phenomenology of shared embodiment and emerging minimal selfhood in pregnancy, has been addressed elsewhere in the literature in length (Young 2005, Smith 2016, Lymer 2011; Moran 2017; Ciaunica 2017; Ciaunica& Crucianelli 2019; Quintero & de Jaegher 2020).

In what follows we restrict our focus on the relationship between co-embodiment and homeostatic and allostatic self-regulatory bodily processes at their earliest manifestations.

3 Modelling the self *through* an other: homeostasis and allostasis under active inference

As we mentioned in the Introduction, one core aspect of the PP/AIF's⁶ take on understanding perception, cognition and action is that our ongoing perceptual experiences are infused by and constructed via prior beliefs (Friston 2005; Clark 2013; Hohwy 2013). These 'expectations' are themselves inherited and probabilistically extracted from dynamic interactions with the environment (e.g., I expect lights to turn on when I flip the switch up because flipping the switch upwards turns on the light on the light more often than not, in the sort of world in which I live). If this hypothesis is correct, then it is essential for AIF to consider 'expectations' or the 'predictions' through an early developmental lens. This is because the way the 'first priors' are acquired will fundamentally influence the way individuals' perceptions, cognition and consequent actions will dynamically unfold throughout one's life, and influencing thereby their higher-level decision-making strategies. Importantly, the claim is not that these 'first priors' have long term causal effects on adult life⁷. Rather, to paraphrase Clark's famous formulation: the claim is that whatever comes first influences whatever comes next. Hence, the adult-centric perspective on understanding embodiment and perceptual experiences needs to make room to a more inclusive and ecological approach, one that takes into account the characteristics of these early perceptions and their impact on one's experiential life.

As we say earlier, the hallmark of PP and AIF theories is that humans are essentially self-organising biological agents. The notion of 'self-organisation' has been addressed extensively in philosophy and theoretical biology in order to explain how biological systems – such as human bodies – resist the natural tendency to disorder (Conant and Ashby 1970).

⁵Note that pregnancy is not the only case where we can find instances of strong co-embodiment (e.g. Siamese siblings). Here we will focus on the case of pregnancy because of its universal prevalence: to date, all humans have shared their body with another human being in this strong co-embodied sense. ⁶The past decades have seen a flood of research on Predictive Processing and Active Inference frameworks and their close relationship

^oThe past decades have seen a flood of research on Predictive Processing and Active Inference frameworks and their close relationship (for a review see Friston, 2010, 2018). Some authors have proposed that the latter is an enactive formulation of the former (Ramstead et al., 2019). Note that the proposed general description here may fit both a predictive processing and active inference reading. Given that the literature we appeal in the remainder of this paper has been developed mostly under an active inference reading, our appeal to the co-embodiment and co-homeostasis theses refers to AIF (but fits into the PP reading as well). We are grateful to an anonymous reviewer for pressing clarification on this point.

⁷Proponents of the so-called 'attachment theories' argue that the way infants attach to their caregivers in their early life strongly impacts the way individuals attach to other individuals throughout their adult life (see Ainsworth et al. 1978)

There are at least three key routes to acquire and finesse expectations for optimally computing self- and world-models: (a) by changing (updating) the model to better account for incoming sensory inputs (*perceptual inference*) (Friston et al. 2006); (b) by selectively sampling sensation that can be accounted for by the model (*active inference*) (Pezzulo et al. 2015); (c) by directly changing, implicitly and explicitly, the statistical structure of the environment in a way that allow accurate prediction of future sensory inputs (e.g., through *cognitive niche construction* (Constant et al., 2018; 2020). Perceptual inference reduces our uncertainty about what caused our sensory observations via updating one's internal model of the world. By contrast, selective sampling moves the sensory organs so as to capture expected sensations. Finally, cognitive niche construction changes the environment with the aim of better informing prediction in the future. These three processes are geared towards organising and updating expectations about (i) the self, (ii) the world and (iii) its relation to the world (Adams et al. 2013; Friston et al. 2017).

Crucially for our discussion here, these three routes to the optimisation of expectations in the generative self- and world-models have been put forward to explain the processes of *homeostasis*. Homeostasis refers to the organism's need to maintain a stable internal environment despite fluctuating external environment and homeostatic regulation entails using feedback control mechanisms to keep sensed variables of the internal environment within ranges compatible with survival (Modell et al., 2015). It is well-established that this control involves automatic actions (e.g. motor reflexes, endocrine, immunological, and autonomic processes) that are driven by feedback inputs and the resulting "prediction error" — the discrepancy between an expected bodily state (a homeostatic setpoint) and its actual level as signalled by sensory inputs from the body (Modell et al., 2015).

The underlying assumption is that fundamental drive towards self-preservation is essentially linked to the constraints acting upon the body's visceral states. Hence, it has been proposed to define homeostatic setpoints as the expectations (means) of prior beliefs about the states the body should inhabit, and homeostatic range as the variance of these prior beliefs (Stephan et al. 2016). Indeed, a central thesis is that the control of bodily homeostasis constitutes a primary aim of brain function (Cannon, 1929).

Previous research has examined error-based reactive control in relation to several vitally important variables (such as blood acidity, body temperature, blood levels of glucose and calcium, plasma osmolality) (Woods and Wilson, 2013) and has mapped the anatomy and

⁸"Under very broad conditions, that any regulator that is maximally both successful and simple must be isomorphic with the system being regulated. [...] The theorem has the interesting corollary that the living brain, so far as it is to be successful and efficient as a regulator for survival, must proceed, in learning, by the formation of a model (or models) of its environment." (Conant and Ashby 1970 : 89).

Conscious Cogn. Author manuscript; available in PMC 2021 November 25.

physiology of neuronal circuits. It has been argued that while this reactive type of control dominates the classical literature on homeostasis, it likely only represents the lowest layer in a hierarchy of temporally extended control mechanisms, with most immediate consequences.

However, from an embodied and situated cognition perspective, the brain needs to build an accurate and updated model of not only of (1) bodily states, but also (2) the external environment, and the (3) bi-directional relation between the two. Hence, higher levels that enable prospective control are leveraged, with two essential components: inference (on current bodily state) and prediction (of its future evolution, on its own and in response to chosen actions) (Penny and Stephan, 2014; Pezzulo et al., 2015; Seth, 2015). In a nutshell, homeostatic regulation requires a model that enables inference (perception) and prediction (action selection). Importantly however, the brain initiates regulatory responses prior to a homeostatic alteration, provided it can be anticipated (Sterling, 2012).

This brings us to *allostasis*. Allostasis, or anticipatory homeostatic control is a kind of extension of homeostatic control in at least two ways. First, allostasis is regulation via pre-emptive change of the parameters of one system to regulate another system (hence it entails modelling to represent a series of actions or, regulation consequences). It is a way to seek "stability through change" (Sterling, 2014). Second, allostatic control has a hierarchical nature. As allostasis achieves regulation in monitoring more than one system that may be in conflict for the organism's resources, it entails hierarchical modelling of predictions at higher levels that can 'explain away or, regulate' prediction errors at the various systems at stake lower in the hierarchy. The notion of model-based allostatic regulation builds again upon the seminal work by Conant and Ashby (1970) stipulating that brain requires a model of the external world in order to implement optimal control. Under active inference framework, allostasis just is the process whereby agents select actions that will most probably bring about the desired sensory entries, while explicitly or implicitly modifying the true causal structure of the environment, so as to guarantee the recurrence of those inputs over multiple time steps (Ramstead et al. 2019b). Allostasis is not merely action in the service of maintaining homeostatic setpoints. Allostasis is also the active control of setpoints in response to environmental demands⁹.

It has been proposed that the basic experience of being a self is the result of an ongoing inferential process based on a generative model centred onto the self (Seth 2013; Apps & Tsakiris 2013; Limanowski & Blankenburg 2013; Limanowski and Friston 2018, 2020). From an AIF point of view, this begs a fascinating and unanswered question: "what does it mean for an organism to embody a model of another organism, the optimisation of which makes up one's own homeostasis?". How exactly do two brains and bodies, at different stages of their life course, manage to regulate their internal parameters through modelling a shared biological milieu? These are important and difficult questions that we can only hope to begin to highlight here, and need to be systematically addressed in future research (**Author, under review). In this paper we restrict our focus on drawing attention on the fundamental state of (co)-embodiment and its relationship with homeostatic and allostatic processes through the AIF theoretical lens.

⁹We are grateful to an anonymous Reviewer for helping clarifying this point.

Conscious Cogn. Author manuscript; available in PMC 2021 November 25.

The pregnancy case is extremely interesting for the AIF approaches for at least two reasons: (a) first, as outlined earlier, it is a universal case: all humans had their body emerging within another's body; (b) second, these two bodies are bound to share for a set time period (typically 9 months) common bodily and environmental resources, and hence they are strongly homeostatically coupled. But before we address the key notion of co-homeostasis, let us first have a quick look at the emergence of the self-organising human body within another's body. We turn to this discussion now.

4 Back to square one: the emerging self within an other's body

If we go back to its earliest manifestation, a successfully emerging self-organising system such as a human body needs to meet numerous constraints in order to stay alive and successfully grow. It would be too long to provide here a comprehensive description of the fascinating journey of the human life within a womb (see Piontelli, 2010; Quintero & de Jaegher 2020 for a more detailed discussion). Yet, it is important to draw the backbone of the emergence of the human organism as a key step in exploring further how perception, cognitive processes and primitive actions get off the ground in the first place.

The aim is to show that unlike the traditional view that considers the mother's body as a mere passive 'recipient' designed to contain the growing baby, empirical evidence speaks in favour of an active and bi-directional co-regulation between the two organisms (Quintero & de Jaegher 2020). Pregnancy is a state in which two organisms actively negotiate common shared bodily and environmental resources. And like any other precarious negotiation, things can go wrong (leading to disease, malformations and even death), or it can lead to a successful outcome: a healthy baby and a healthy mother.

A good place to start is the process of *egg implantation* which is one of the biggest challenges to set up pregnancy as shown by clinical studies reporting that around 75% of pregnancy losses occur at this stage (Cha et al., 2012, Norwit et al. 2001). Assuming that the embryo and the receptive endometrium are fully functional, they have a very narrow window to coordinate the implantation process (Cha et al., 2012; Teklenburg et al. 2010). This bi-directional coordination is a delicate and crucial process as noted by Quintero & de Jaegher:

"both blastocyst and endometrial tissues actively regulate gene expression, transcription factors, signalling pathways, inhibiting factors, and growth factors during the implantation process. (...) The maternal body literally self-modifies some of its cells, through differentiation, into specific types that support implantation: namely decidual stromal cells, uterine natural killer cells, and macrophages (Nuño de la Rosa et al. 2019). In turn, the embryo needs to coordinate with these specialised cells within the implantation window" (2020:7).

Immediately after implantation, another key stage unfolds: in order to successfully 'hold' or to maintain the grip of the embryo in the epithelium, the maternal organism needs to flexibly adapt its physiological systems in order to incorporate them into her homeostatic and metabolic processes. In other words, maternal nervous, cardiovascular, locomotor, and immune systems will adjust in order to 'sustain' the embryo's grip and development.

If the coordination between the embryo and the uterine cells is successful, then the process is taken at the next step of self-organisation which involves movement. Between week 7 and 13 most movements are initiated from the so-called 'central pattern generator'¹⁰ in the early spinal cord which produces around week 8 abrupt, startles of the entire foetal body (Piontelli, 2010).

The first self-generated movements of a new human organism – as revealed by abdominal ultrasound – occur towards the end of embryogenesis (in the seventh gestational week) (see Einspieler et al. 2012). By eight gestational weeks, rotation and displacement of the thorax and limbs are observed (de Vried et al. 1982; Lüchingen et al. 2008; Piontelli 2010).

Importantly, the startles provide the minimal basis for the most basic occasions of sensory feedback: "a hand may start to touch the face, or a leg may change its position, be flexed or extended, or both" (Piontelli 2010: 23). Minimal sensory feedback at this stage affords the possibility to respond and adapt to these movements. This means that self-organisation in foetal movement initiates as a biomechanical process that progressively builds sensitive and regulatory capacities. For example, while being stimulated by a startle, the foetus perceives his hand as movable, and that touching the face rather than the uterine wall with the hand is more sensitive. In short, "through general movements foetuses begin to 'learn' to move and to attune their motions" (Piontelli 2015:128).

Previous work showed that sensorimotor behaviour displays, even before birth, an anticipatory structure, despite the fact that these early actions are not cognitively sophisticated (Trevarthen 1984; Lee 2005; Legrand 2006; von Hofsten 2004; Delafield-Butt & Gangopadhyay 2013). There seems to be a close link between body movements and sensation-seeking properties of basic actions, which is essential for perceptual learning (Thelen & Smith 1994; Gallagher 2005; Pezzulo 2011; Reddy 2008). For example, developmental studies show that neonates will move their arms to explore sensory effects (van der Meer 1997). These self-generating actions are "orchestrated prospectively to make use of inevitable biomechanical consequence of action synergistically" (Delafield-Butt & Gangopadhyay 2013: 405).

At a later stage (eight to ten weeks of gestation), foetal arm movements are directed to the body, with preference to the face and head. Crucially, at this point of development, certain bodily parts are innervated with sensory nerve fibres (e.g. lips, cheeks, the parietal bone), and foetuses frequently touch these areas with their fingers, which are in turn richly innervated¹¹. As Delafield-Butt & Gangopadhyay note:

¹⁰The central pattern generator is responsible for producing also the rhythmic patterns of breathing movements which are independent of maternal breathing (Piontelli 2010, ten Donkelaar et al. 2014). It has been proposed that "foetal breathing movements can be considered an emerging sensorimotor coordination as they: (1), produce mutually enabling conditions, (2), define themselves as a system separated from, yet interacting with other systems, and (3) modulate their relation with the medium by equilibrating—accommodating and assimilating—fluid density, space, and pressure." (Quintero & de Jaegher 2020: 9). ¹¹The self-exploratory tactile behaviour of foetuses in the womb may be regarded as a key example of perception *as* action

¹¹The self-exploratory tactile behaviour of foetuses in the womb may be regarded as a key example of perception *as* action (Noë 2004). Crucially however, self-exploratory movements, as well as amniotic composition and pressure covaries with maternal metabolism, movement and clinical conditions. For example, if the mother is completely static (because she has a spine injury and cannot move) then certain perceptions and self-exploratory movements dependent on the other's perceptions, bodily physiological processes and movements. We are grateful to an anonymous reviewer for pressing clarification on this point.

"These touches to sensitive innervated regions create an autostimulatory feed-back loop, where the action creates contact between the fingers and head, giving simultaneously a proprioceptive response in the resistance met at contact, the sensation of touch in the fingers, and the sensation of touch in the innervated region. Foetuses have been observed exploring the boundary of the innervated and uninnervated regions, particularly at the anterior fontanel of the forehead where innervation ceases. As the nervous innervation of the forehead increases and the boundary migrates during development, so the foetus' exploration of this region migrates with the boundary, demonstrating the foetus was not merely exploring a spatial region, but the special relationship between differences in autostimulatory feedback either side of the boundary of innervation (Piontelli, 2010, pp. 61–67) " (2013:405).

Indeed, it has been proposed that "the first generation of experiential knowledge (...) establishes an embodied foundation for further learning the specific sensory consequences arising from external forces by external 'objects', and the process of learning from prospective action" (Delafield-Butt & Gangopadhyay 2013: 405)¹². Frequently observed movements such as 'bicycling the legs, swinging one's body in the womb, touching the placental lining and the umbilical cord, seem to suggest that we are in presence of an enacted degree of precision that presupposes coordinated prospective control. Further evidence for this hypothesis comes from twin studies.

For example, Castiello and colleagues (2010) examined the kinematic profiles of movements in five pairs of twin foetuses by using four-dimensional ultrasonography during two separate recording sessions carried out at the 14th and 18th week of gestation. They showed that by the 14th week of gestation twin foetuses do not only display movements directed towards the uterine wall and self-directed movements, but also movements specifically aimed at the co-twin, the proportion of which increases between the 14th and 18th gestational week. Kinematic analysis revealed that movement duration was longer and deceleration time was prolonged for other-directed movements compared to movements directed towards the uterine wall. They also observed similar kinematic profiles were observed for movements directed towards the co-twin and self-directed movements aimed at the eye-region, i.e. the most delicate region of the body. They concluded that performance of movements towards the co-twin is not accidental: already starting from the 14th week of gestation twin foetuses execute movements specifically aimed at the co-twin. This has been reported in singleton pregnancy as well, where kinematic studies seem to suggest that motor planning is in place by 22 weeks of gestational age (Zoia et al. 2007).

The fascinating biophysical process of becoming a 'self' within an other's body cannot be addressed here in detail. For our purposes here it is important to retain that despite the widespread view of foetal movements as random and disorganised reflexes, it has been suggested that even the simplest movement can be considered a sensorimotor event and *self-organised* (Thelen and Smith 1994). These movements emerge from the co-regulation

¹²Interestingly, as noted by Delafield-Butt & Gangopadhyay, "patterns of behaviour appear to confirm a continuum of agency specific to that individual. For example, Piontelli reported idiosyncratic behavioural consistencies from foetal to childhood life (Piontelli, 1992; Piontelli, 2002) and Beckoff noted a functional continuity between foetal 'play' and childhood play (Bekoff et al., 1980)" (2013: 405).

Conscious Cogn. Author manuscript; available in PMC 2021 November 25.

between (i) early nervous system, (ii) the foetal body support structures (muscles, bones, organs), and (iii) elements of the uterine environment (fluid density, structural support, pressure, available space, etc., (Mori and Kuniyoshi 2010, Smotherman & Robinson 1988).

Crucially, these movements do not occur in a vacuum: amniotic composition and pressure covaries with maternal metabolism, movement and clinical conditions (Wallace, et al. 2015). As Lymer nicely puts the point:

"the situation of a 10 week old foetus within a fluid-filled womb within a moving body amidst rhythmic beatings and breathing would facilitate a continuously moving, flowingly rhythmic world. The growing buoyant weight of the foetus at this early stage would precipitate the rolling and rocking movements that are fundamental to develop capacities for basic homoeostatic bodily positioning such as upright and sideways" (Lymer 2011:139).

Future work needs to explore in more details the allostatic regulation achieved through the placenta from a biophysiological perspective (**Author et al., in prep). In the remainder of this paper however we argue that the fundamental co-embodied nature of the metabolic processes makes the self-organisation of the emerging organism strongly dependent (in the sense defined above) upon another organism's homeostatic and allostatic processes. Given the necessary co-embodiment sustaining the human body's self-regulation and self-organisation from the outset, the early homeostatic regulation should thus be fundamentally conceived relationally as co-regulation, and hence *co-homeostasis*.

5 From Co-Embodiment to Co-Homeostasis

As we saw earlier, both embodied and PP/AIF approaches rightly point out to the role of the organism's physical and social environment and cognitive niche in understanding the constitutive relationship between self-organising systems (such as human bodies) and their physical and social environment (Varela et al. 1991; Fotopoulou & Tsakiris, 2017; Seth & Tsakiris 2018). However, less attention has been paid to the idea that human bodies necessarily emerge within another human body (co-embodiment) (Ciaunica and Crucianelli 2019). For a set time period (typically 9 months), two (or more) self-organising organisms are bound to share bodily and environmental resources in order to survive. How does this primordial co-embodiment affect homeostatic self-regulatory processes?

Two points are worth noticing before we move further. (1) First, in the individual living organism, homeostatic processes (mostly innate and evolutionarily hardwired) and allostatic processes (mostly acquired and flexible) are like the two faces of the same coin. This is because, as we outlined earlier, humans are dynamic beings, dependent on rich environmental resources and social interactions to achieve survival and reproduction. Perception and action, homeostatic and allostatic self-regulation are coupled in a dynamic loop that keeps the organism permeable to and connected with its surroundings (for better and for worse)¹³.

¹³Perhaps the most striking example in favour of the necessary distinction between homeostatic (automatic) and allostatic (controlled) self-related processing comes from conflict cases. For example, an individual that decides to commit suicide, may do so by taking toxic pills, but cannot do so by ordering his/her cells to stop self-regulating. In the case of suicidal actions, the self-organising

Conscious Cogn. Author manuscript; available in PMC 2021 November 25.

(2) Second, in pregnancy, the self-regulatory architecture is multi-layered: the baby's regulatory processes are coupled with the mother's homeostatic-allostatic processes. This is achieved mainly through the placenta – an ephemeral and intermediary organ that enables vital, biological exchanges between two bodies. For example, it allows the infant to breathe despite lacking proper lung regulation and ensures the infant is fed despite lacking proper eating effectors. Placenta is a relational organ *par excellence*, and also a universal organ. Future work needs to address the key role of this fascinating organ (see Burton et al. 2015; **Author et al. in prep), but here we restrict ourselves here to highlighting that the placenta, like the later developed human skin, acts both as a barrier and a connector allowing nutrients, gases, hormones and wastes to pass between the co-regulating organisms but also ensuring that neither's immune system treats the other as a foreign to be attacked organism.

This draws our attention to what is happening *in between* the two organisms. In line with the AIF approaches, it is important to bear in mind that homeostatic and anticipatory self-regulation depends not only on (a) bodily states, but also (b) the external environment, and crucially on (c) *the relation between the two*. We can thus define *co-homeostasis* as the bi-directional process of co-regulation that happens *in between* two co-embodied organisms. Co-homeostasis involves self-regulation *through* the other's homeostatic and allostatic coupled states.

How does this work? Traditionally, it has been assumed that the foetus has no metabolism of its own. Nowadays it is well established that the placenta and foetal liver work in tandem as a coordinated multi-organ system to provide the necessary nutrients subserving the foetal metabolism and growth (Anderson et al. 1997; Bataglia 2000; Vaughan & Fowden 2016) Significant attempts have been made to understand the foetal metabolism in a very low oxygen environment (pO2 16-27 mmHg) – the so-called 'Mount Everest in utero' concept. Glucose is the most important fuel for foetal metabolism and ultimately homeostasis. Indeed, maintaining an optimal balance of continuous supply of nutrients from the mother to the foetus is critical for development. There is accumulating evidence for a direct link between mothers' adverse bodily and mental health states (depression and anxiety) during pregnancy and the child's mental and physical development (see Schetter and Tanner 2012; Bauer et al. 2020 for reviews). This holds also for neutral states such as food preferences and flavours (Birch 1999; Mennella et al. 2001; Venter et al. 2009) which are passed along from mother to the infant.

The state of co-embodiment leaves room to a certain degree of bi-directionality. For example, mother and foetus, through repeated trial and error, learn to mutually coordinate meals times and other embodied needs. Mothers may use signals from their body to allostatically regulate their own and hence the foetus' feeding schedule, ensuring thereby regulation of key nutritional variables before some of the infant's homeostatic mechanisms kick in. As such they shape their foetus' homeostasis (close the loop in homeostatic models) and they co-build their allostatic regulatory models (which allow learning and anticipatory models to be built).

organism will fight until the last minute for self-survival, despite the fact that the individual voluntarily took action against selfpreservation. We are grateful to one anonymous Reviewer for pressing clarification on this point.

Conscious Cogn. Author manuscript; available in PMC 2021 November 25.

A classic example here is energy homeostasis in development, within and outside the womb. In everyday life we sometimes feel 'hungry'. However, we do not eat because our blood sugar (glucose level) is low (homeostatic feedback regulation), but rather we reduce blood sugars *before* habitual meal times, in anticipation of the increased post-meal blood sugar intake (allostatic feedforward control). The regulation of eating is thus done around long-term fat (adiposity; and related hedonic and social incentives in the environment), not just everyday feelings of internal hunger, as we intuitively believe.

Note that bi-directionality does not necessarily mean a perfect symmetry in co-regulation, nor the absence of conflict. Importantly, bi-directionality does not mean that the exchanges between the two organisms need to be symmetrical¹⁴. To use a metaphor: think of a two ways motorway travelling north to south (and vice versa). The traffic may be busier from north to south, say (more vehicles are circulating in that direction). However, if one single car travels from south to north, the route *is* bi-directional. For example, the discovery that bi-directional cell trafficking results in persistence of foetal cells in the mother and of maternal cells in her offspring for decades after birth (Bianchi et al. 1996; Maloney et al. 1999; Nelson 2008) has shed new light on what is called the "pregnancy's long-term legacy" (Adams Waldorf & Nelson 2008). Specifically, it has been observed the long-term persistence of a small number of cells (or DNA) from a genetically disparate individual, a phenomenon called "microchimerism". As Adams Waldorf and Nelson (2008) note, while microchimerism is common in healthy individuals and is likely to have health benefits, microchimerism can been implicated in some autoimmune diseases such as systemic sclerosis, leading to negative effects.

It is true that during pregnancy, the mother controls the interactions with the external physical and social environment based on her prior, and more advanced allostatic regulation, and as such, she sets up many of the baseline states for the infant's mainly homeostatic regulation. To use again our metaphor: the traffic is busier from north to south. Yet, these systems communicate and exchange information, even if only one has the meta-agentic control. For example, the foetus may be able to control and 'save' energy to some extent through many complex, dynamic processes. Also, the foetus' discomfort may manifest as a kick in the uterine wall. Consequently, an optimally responsive pregnant person may engage in regulatory behaviour, such as drinking water, walking, touching the belly or changing posture. The foetus thus can progressively learn and anticipate that kicking will be accompanied by physiological changes. Thus, reflexive actions come to be slowly learned as capable of fulfilling physiological predictions.

Now, the degree to which foetus in the womb have such allostatic control is unknown, but one may speculate that homeostatic mechanisms dominate and most of the allostatic load falls into the mother's body. For example, the foetus's sugar levels are regulated via the placenta. And the mother body, based on her allostatic regulation changes its adiposity in order to regulate the placenta, which is the organ responsible also for protecting the mother biology from harmful exposures to the foetus and vice versa. Importantly however, note that it is oversupply or undersupply of nutrients – that is, processes controlled by

¹⁴We are grateful to one anonymous reviewer for pressing clarification on this key point.

Conscious Cogn. Author manuscript; available in PMC 2021 November 25.

the pregnant person – can permanently program the foetal metabolism adversely. Hence, the emerging self-organising system (human organism) is not only 'self-centered', but also crucially co-embodied and co-dependent upon the other's homeostatic processes within the uterine environment.

One major open question to be addressed in future work is whether the foetus is able to generate self- and world-models, and if yes, at what stage of the neural and bodily development. In other words, what is the neural substratum of early perceptual and conscious experiences *in utero*? A detailed discussion of this fascinating question would lead us to a substantial digression and has been addressed in a dedicated paper (**Author et al. submitted). Here we propose a brief overview of the most relevant milestones of neural development.

Previous work suggests that the cervical spinal cord nuclei are rapidly forming axodendritic synapses, initially between interneurons and motor neurons, then between afferent fibres and interneurons at seven weeks gestational age. The 'special visceral nuclei' of the brain are formed and becoming innervated providing the basis for subsequent sensorimotor control (Trevarthen, 1985). Later on, the appendicular skeletomusculature with sensory and motor nervous connectivity to the spinal column and brain stem nuclei for basic proprioceptive motor control (Okado, 1980) is in place at around eight weeks gestational age. At this stage however, the forebrain is not yet fully developed, and the neocortex is not yet organised (Larroche, 1981) with the thalamocortical projections being still immature (Hevner, 2000).

Speculatively, the foetal brain may be in possession of the basic tools to generate selfand world-models only after the basic thalamo-cortical connections are established in the foetal brain (it starts around the 20th week of gestation). Only at this time point sensory information can be transferred to the foetal brain. Indeed, corticospinal projections do not reach the cervical spinal cord until twenty-four weeks gestation (Eyre et al. 2000). Before the establishment of the thalamo-cortical connections, the foetus just acts on a reflex, automatic mode. However, the central pattern generator, the seemingly "chaotic" yet exploratory movements are necessary for the development of a correct somatosensory-motor coupling for later life. Again, this is also only possible after the 20th week of gestation. What does this mean for the homeostasis thesis proposed here?

Taking into account the different trajectories of foetal brain development, it has to be stressed that the hypothalamus develops during early stages (starting around week 9). This poses the possibility that homeostatic control may be in place during this early developmental period. In a nutshell, systems such as the spinal column, brain stem, and midbrain (i.e. phylogenetically ancient brain structures, well-known for visceral organ regulation and sensory and motor information transmission) may play a key role in sending sensory information from inferior visceral and somatic receptors to superior cortical function via the corticospinal tract.

However, the foetus is not able to determine in any way the nutritional supply. The foetus completely relies on the nutritional support by the mother and regulatory processes control the distribution of nutrients. This means that the equilibrium point is determined by the

external energy and already implies a distorted equilibrium point, possibly a set point which is imprinted during development. Taken this into account, it is possible that during early development until the thalamo-cortical connections are in place the foetal-maternal co-embodiment involves a "homeostatic foetus" and an allostatic pregnant mother. However, allostasis in the foetus can develop after gestational week 20. Why should foetal allostasis develop? The in-utero environment and even the pre-conception condition can lead to alterations in the organ function and crosstalk which make the offspring susceptible for further diseases. It may be favourable if allostasis would develop at this time, but further work needs to determine how exactly these processes are implemented.

Future Directions

The co-embodiment and co-homeostasis theses that we have outlined here may have important implications on several critical questions fuelling current debates on the nature of perceptual experiences, consciousness and minimal self-awareness. While a detailed discussion of these implications lies beyond the scope of this paper and is to be addressed in dedicated paper (**Author et al. submitted), it is important however to outline what we take to be the most seminal ones.

First, as we saw earlier, a dynamic and complex system such as the human body needs to be able to play a double game, so to speak, in order to survive and potentially reproduce: (a) it has to successfully maintain sensory states within certain physiological bounds; (b) to flexibly change these states in order to adapt a constantly changing environment. If we look at the human body through this dynamic lens, it become obvious that what happens *in between* the organism and its environment – i.e. the boundaries – plays a key role in making sure this game is played successfully and flexibly enough to maintain the organism alive. Future work thus needs to define the critical notion of "boundary" or "in between", i.e. the process of exchanges between two states or two organisms.

The notion of 'Markov blanket' has been recently advocated as a potential candidate providing a promising way of conceptualizing the key notion of boundary or medium underlying the interactions between a system and its environment (Pearl 1988; Kirchhoff et al. 2018; Palacios et al. 2020). Again, this complex question is to be developed in a dedicated paper (**Author et al. submitted). However, let us note briefly that a Markov blanket can be roughly described as a statistical boundary that separates two sets of states. One seminal example is the cellular membrane separating intracellular and extracellular dynamics. The boundary not only separates the system from its environment, but also, importantly, is inherently relating the system to its environment. Crucially, the notion of boundary is as essential as the system and its environment itself (Sims 2020). Indeed, it plays the key role of distinguishing (separating) yet simultaneously relating the organism with his niche. As we hopefully illustrated throughout this paper, this intrinsically dual function— to separate *and* to relate— of the ephemeral boundary organ (the placenta) can be prominently seen at work in the case of the co-embodiment during pregnancy.

A second key implication concerns the very definition of the term 'minimal self' and 'minimal self-consciousness' (**Author et al. submitted). Indeed, while previous approaches

tackled this issue by attempting to identify the fundamental basis of minimal selfhood (i.e. its unchangeable immutable structure across all conscious experiences) (Zahavi 2005; Blanke & Metzinger 2009), another alternative is to focus on the contrary on how selfhood and conscious experiences get off the ground and dynamically unfold across one's lifespan. To use a metaphor, 'minimal' in this sense would refer to the seed that contains all the latent information about the upcoming tree, rather than the schematized, abstract shape of a fully-fledged adult tree.

Third, endorsing a developmental lens in understanding our embodied minds may help us address the perennial mind-body problem on fresh grounds. For example, how the mindbody problem would have been formulated if the French philosopher and scientist René Descartes was a pregnant Renée? (**Author et al. under review).

A further question concerns the nature of our conscious experiences and the tacit vision bias of current theories of consciousness (Faivre et al. 2017). In its seminal paper 'Whatever next? Predictive brains, situated agents, and the future of cognitive science' Andy Clark (2013) proposed that our brain's job is to predict whatever information is coming 'next' on the basis of the prior information perceived before. In line with this approach, one may argue that term 'next' should be understood not only at the temporal scale (i.e. what is perceived in the upcoming second); but also, from a spatial dimension (i.e. what is perceived literally *next to or close-to-my-body*). This is because the survival of the organism critically depends on accurate and optimal information processing not only in the 'now', but also in the 'here' (as opposed to a distal 'there'). In other words, we need to examine with high priority the perceptual processing of *proximal* sensory inputs (such as smell, touch, proprioception and visceral signals) which have a key impact on our survival (**Author et al. under review).

Finally, further work needs to highlight the special role of touch and tactile experiences in the orchestration of our conscious experiential life, as illustrated by the studies mentioned above showing that foetuses spend a considerable amount of time tactilely exploring – with their richly innervated fingers - the boundaries between the innervated parts of their bodies (lips, cheeks, etc.) and the less innervated ones. There are at least three interrelated main reasons for that. (1) First, touch is mediated by the skin, the oldest and widest organ in terms of dimensions and functions (Montagu 1971; Field 2001). By providing the organism with the most primitive means to 'meet' and perceive the world, tactile experiences may constitute thereby the most ubiquitous and basic (i.e. minimal) experiential background (Ratcliffe 2013; Ciaunica & Crucianelli 2020). (2) Second, the skin mediates the boundary between the self and the outer world, and as such, tactile experiences display an inescapably dual 'touchant/touche' structure to use the seminal Merleau-Ponty's (1945) expression. By gaining information about the world via touch, the subject inherently gains information about her 'self' too. (3) Last but equally important, touch plays a key exploratory and bonding role, which confers it a sense of 'closeness' and 'presence' or realness: we touch things to make sure they are real and we touch people to communicate profound emotions (for example, we hold someone's hand to alleviate their pain and grief) (Gallace & Spence 2010; Cascio et el. 2019).

Conclusion

In this paper we looked at the basic yet overlooked idea that the human body is a selforganising organism that emerges and develops *within* another human body. This is what we called the co-embodiment thesis.

We argued that the state of co-embodiment leads necessarily to co-homeostasis defined as the bi-directional process of co-regulation between the two (or more) co-embodied organisms. Co-homeostasis in human primitive bodies relies upon self-regulatory processes achieved *through* others' homeostatic and allostatic coupled metabolic processes. This is because, for a set time period (typically 9 months), two human bodies actively negotiate bodily and environmental resources and need to share biophysiological information in order to successfully sustain survival of both organisms. The pregnant state is thus a precarious and bi-directional (although asymmetrical) negotiation, that can lead to negative (disease and death) or positive outcomes (health and new life).

We suggested that the Active Inference approach may be regarded as a promising framework to address in computational terms the story of this negotiation. We built upon a significant body of work in the context of active inference highlighting the close link between self-organising systems and their close environment and the free energy principle (Friston 2005; Clark 2013; Hohwy 2013). Since, as we hopefully illustrated throughout this paper, human beings do not come into existence in an individualistic and solipsistic fashion, further work is in need to examine the impact of the co-embodiment and co-homeostasis theses on perennial philosophical and scientific questions such as the mind-body problem, the nature of conscious experiences and the minimal self.

This paper's main aim was to highlight that sharing our first 'prior' or primitive embodied states is fundamental and universal: it concerns, to date, all humans. Future work needs to address the key question: what is the impact of this primitive and fundamental shared co-embodied states on the human mind workings and social cognition more generally?

References

- -. Adams RA, Stephan KE, Brown HR, Frith CD, Friston KJ. The computational anatomy of psychosis. Frontiers in psychiatry. 2013; 4 :47. [PubMed: 23750138]
- -. Adams Waldorf KM, Nelson JL. Autoimmune disease during pregnancy and the microchimerism legacy of pregnancy. Immunological investigations. 2008; 37 (5):631–644. [PubMed: 18716941]
- -. Allen, M, Tsakiris, M. The Interoceptive Mind: From Homeostasis to Awareness. First Edition. Oxford University Press; 2019. 27–45.
- Anderson AH, Fennessey PV, Meschia G, Wilkening RB, Battaglia FC. Placental transport of threonine and its utilization in the normal and growth restricted fetus. American Journal of Physiology. 1997; 35 :E892–E900.
- -. Apps MA, Tsakiris M. The free-energy self: a predictive coding account of self-recognition. Neuroscience and Biobehavioral Reviews Apr. 2013; 41 :85–97.
- Atzil S, Barrett LF. Social regulation of allostasis: Commentary on "Mentalizing homeostasis: The social origins of interoceptive inference" by Fotopoulou and Tsakiris. Neuropsychoanalysis. 2017; 19 (1):29–33.

- -. Bauer I, Hartkopf J, Kullmann S, Schleger F, Hallschmid M, Pauluschke-Fröhlich J, Fritsche A, Preissl H. Spotlight on the fetus: how physical activity during pregnancy influences fetal health: a narrative review. BMJ Open Sport Exerc Med. 2020 Mar 16. 6 (1) e000658
- -. Battaglia FC. Glutamine and glutamate exchange between fetal liver and the placenta. Journal of Nutrition. 2000; 130 (4S Suppl) :974S–977S.
- -. Bekoff M, Byers JA, Bekoff A. Prenatal motility and postnatal play: Functional continuity? Developmental Psychobiology. 1980; 13 (2) :225–228. [PubMed: 7358223]
- -. Berlucchi G, Aglioti SM. The body in the brain: Neural bases of corporeal awareness. Trends in Neurosciences. 1997; 20:560–564. [PubMed: 9416668]
- -. Bianchi DW, et al. Male fetal progenitor cells persist in maternal blood for as long as 27 years postpartum. Proc Natl Acad Sci U S A. 1996; 93 (2) :705–708. [PubMed: 8570620]
- -. Blanke, Olaf. Multisensory brain mechanisms of bodily self-consciousness. Nature Reviews Neuroscience. 2012; 13:556–571. [PubMed: 22805909]
- -. Blanke O, Metzinger TK. Full-body illusions and minimal phenomenal selfhood. Trends in Cognitive Sciences. 2009; 13 (1) :7–13. [PubMed: 19058991]
- -. Blanke O, Slater M, Serino A. Behavioral, neural, and computational principles of bodily selfconsciousness. Neuron. 2015; 88 (1) :145–166. [PubMed: 26447578]
- -. Burton, GrahamJ; , et al. What is the placenta? American Journal of Obstetrics & Gynecology. 2015; 213 (4) :S6.e1–S6.e4. [PubMed: 26428504]
- -. Cascio CJ, Moore D, McGlone F. Social touch and human development. Developmental Cognitive Neuroscience. 2019; 35 :5–11. [PubMed: 29731417]
- -. Castiello U, Becchio C, Zoia S, Nelini C, Sartori L, Blason L, et al. Wired to Be Social: The Ontogeny of Human Interaction. PLoS ONE. 2010; 5 (10) e13199 [PubMed: 20949058]
- -. Ciaunica, A. Pre-reflective Self-Consciousness: Sartre and Contemporary Philosophy of Mind. Miguens, S, Preyer, G, Morando, C, editors. Routledge; London: 2016. 422–438.
- -. Ciaunica A. The 'Meeting of Bodies': Empathy and Basic Forms of Shared Experiences. Topoi. 2017; doi: 10.1007/s11245-017-9500-x
- -. Ciaunica A, Crucianelli L. Minimal self-awareness: From within a developmental perspective. Journal of Consciousness Studies. 2019; 26 (3-4) :207–226.
- -. Ciaunica, A, Fotopoulou, A. Embodiment, Enaction, and Culture—Investigating the Constitution of the Shared World. Durt, C, Fuchs, T, Tewes, C, editors. MIT Press; Cambridge MA: 2017.
- Ciaunica A, Petreca B, Fotopoulou A, Roepstorff A. Whatever Next and Close to my Self The Transparent Senses and the 'Second Skin'. Implications for the Case of Depersonalisation. 2021 Jan 5. doi: 10.31234/osf.io/u8ky6
- -. Cha J, Sun X, Dey SK. Mechanisms of implantation: Strategies for successful pregnancy. Nat Med. 2012; 18 :1754–1767. DOI: 10.1038/nm.3012 [PubMed: 23223073]
- -. Chemero, A. Radical Embodied Cognition. MIT Press; Cambridge, MA: 2009.
- -. Clark A. Whatever next? Predictive brains, situated agents, and the future of cognitive science. Behavioral and Brain Sciences. 2013; 36 (03) :181–204.
- -. Conant RC, Ross Ashby W. Every good regulator of a system must be a model of that system. International journal of systems science. 1970; 1 (2) :89–97.
- Constant A, Ramstead MJD, Veissière SPL, Campbell JO, Friston KJ. A variational approach to niche construction. Journal of the Royal Society, Interface / the Royal Society. 2018; 15 (141) doi: 10.1098/rsif.2017.0685
- -. Constant A, Clark A, Kirchhoff M, Friston KJ. Extended active inference: constructing predictive cognition beyond skulls. Mind and Language. 2020
- -. Damasio A, Damasio H. Minding the body. Daedalus. 2006; 135:15-22.
- -. De Jaegher H, Di Paolo E. Participatory sense-making: an enactive approach to social cognition. Phenomenol Cogn Sci. 2007; 6:485–507.
- -. Delafield-Butt JT, Gangopadhyay N. Sensorimotor intentionality: the origins of intentionality in prospective agent action. Dev Rev. 2013; 33 :399–425.

- -. Eyre JA, Miller S, Clowry GJ, Conway EA, Watts C. Functional corticospinal projections are established prenatally in the human foetus permitting involvement in the development of spinal motor centres. Brain. 2000; 123 (Pt 1) :51–64. [PubMed: 10611120]
- -. de Vries JIP, Visser GHA, Prechtl HFR. The emergence of fetal behavior I. Qualitative aspects. Early Human Development. 1982; 7 :301–322. [PubMed: 7169027]
- -. Einspieler, Christa; Prayer, Daniela; Prechtl, Heinz FR. Fetal behaviour: A neurodevelopmental approach. Mac Keith; 2012.
- Faivre N, Arzi A, Lunghi C, Salomon R. Consciousness is more than meets the eye: a call for a multisensory study of subjective experience. Neuroscience of consciousness. 2017; 2017 (1) nix003 [PubMed: 30042838]
- -. Field, T. Touch. The MIT Press; Boston: 2001.
- -. Fotopoulou A. The virtual bodily self: Mentalisation of the body as revealed in anosognosia for hemiplegia. Consciousness and Cognition. 2015; 33:500–10. [PubMed: 25459651]
- -. Fotopoulou A, Tsakiris M. Mentalizing homeostasis: The social origins of interoceptive inference. Neuropsychoanalysis. 2017; 19 (1) :3–28.
- -. Friston K. A theory of cortical responses. Philosophical Transactions of the Royal Society of London. 2005; 360 :815–36. [PubMed: 15937014]
- -. Friston K. Hierarchical models in the brain. PLoS computational biology. 2008; 4:11.
- -. Friston K, Kilner J, Harrison L. A free energy principle for the brain. Journal of Physiology, Paris. 2006; 100 (1-3) :70–87.
- -. Friston KJ, Stephan KE. Free-energy and the brain. Synthese. 2007; 159 (3) :417–458. [PubMed: 19325932]
- -. Friston K, FitzGerald T, Rigoli F, Schwartenbeck P, Pezzulo G. Active inference: A process theory. Neural Computation. 2017; 29 (1) :1–49. [PubMed: 27870614]
- -. Gallace A, Spence C. The science of interpersonal touch: An overview. Neuroscience and Biobehavioral Reviews. 2010; 34 (2) :246–259. [PubMed: 18992276]
- -. Gallagher S. Philosophical conceptions of the self: implications for cognitive science. Trends Cogn Sci. 2000; 4 :14–21. [PubMed: 10637618]
- -. Gallagher, S. How the body shapes the mind. Oxford University Press; USA: 2005.
- -. Gallagher S. A Pattern Theory of Self. Frontiers in Human Neuroscience. 2013; 7 :443. [PubMed: 23914173]
- -. Gibson, JJ. The Ecological Approach to Visual Perception. LEA; Hillsdale, New Jersey: 1979 / (1986).
- Hall JG. Pena-Shokeir phenotype (fetal akinesia deformation sequence) revisited. Birth Defects Research Part A: Clinical and Molecular Teratology. 2009; 85 (8) :677–694. DOI: 10.1002/ bdra.20611 [PubMed: 19645055]
- -. Hohwy, J. The predictive mind. Oxford University Press; 2013.
- Hevner RF. Development of connections in the human visual system during fetal mid-gestation: A DiI-tracing study. Journal of Neuropathology and Experimental Neurology. 2000; 59 :385–392. [PubMed: 10888368]
- -. Kingma E. Were you a part of your mother? Mind. 2019; 128 :609-646.
- -. Larroche J-C. The marginal layer in the neocortex of a 7 week-old human embryo: A light and electron microscopy study. Anatomy and Embryology. 1981; 162 :301–312. [PubMed: 7270905]
- -. Lee, DN. Action as an organiser of learning. Rieser, JJ, Lockman, JJ, Nelson, CA, editors. Erlbaum; Hillsdale, New Jersey: 2005.
- -. Legrand D. The bodily self: The sensorimotor roots of pre-reflexive self-consciousness. Phenomenology and the Cognitive Sciences. 2006; 5 :89–118.
- -. Lymer J. Merleau-Ponty and the affective maternal-foetal relation. Parrhesia. 2011; 13:126–143.
- -. Lüchinger AB, Hadders-Algra M, van Kan CM, de Vries JI. Fetal onset of general movements. Pediatric Research. 2008; 63 (2) :191–195. [PubMed: 18091359]
- -. Maloney S, et al. Microchimerism of maternal origin persists into adult life. J Clin Invest. 1999; 104 (1):41–47. [PubMed: 10393697]

- -. Merleau-Ponty, M. Phenomenology of Perception. Routledge; London: 1945/2012.
- -. Montagu, A. Touching: The Human Significance of the Skin. Columbia University Press; New York: 1971.
- -. Modell H, Cliff W, Michael J, McFarland J, Wenderoth MP, Wright A. A physiologist's view of homeostasis. Adv Physiol Educ. 2015; 39 :259–266. [PubMed: 26628646]
- -. Moran, D. Embodiment, Enaction, and Culture: Investigating the Constitution of the Shared World. Durt, C, Fuchs, T, Tewes, C, editors. MIT Press; Cambridge, MA: 2017. 25–46.
- Mori, H; Kuniyoshi, Y. A human fetus development simulation: self-organization of behaviors through tactile sensation; 2010 IEEE 9th International Conference on Development and Learning; Ann Arbor, MI. 2010. 82–87.
- -. Nelson JL. Your cells are my cells. Scientific American. 2008; 298 (2) :72-79.
- -. Newen, A, de Bruin, L, Gallagher, S. The Oxford Handbook of 4E Cognition. Oxford University Press; Oxford: 2018.
- -. Noë, A. Action in perception. The MIT Press; Cambridge, MA: 2004.
- -. Norwitz ER, Schust DJ, Fisher SJ. Implantation and the survival of early pregnancy. N Engl J Med. 2001; 345 :1400–1408. [PubMed: 11794174]
- -. Nuño de la Rosa L. Becoming organisms: the organisation of development and the development of organisation. History Philos Life Sci. 2010; 32 :289–315.
- Okado N. Development of the human cervical spinal cord with reference to synapse formation in the motor nucleus. The Journal of Comparative Neurology. 1980; 191 :495–513. [PubMed: 7410604]
- Oppenheim, RW. Maturation and development: Biological and psychological perspectives Clinics in developmental medicine. Connolly, KJ, Prechtl, HFR, editors. Vol. 77. Spastics International Medical Publication; London: 1981. 73–109.
- -. Palacios ER, Razi A, Parr T, Kirchhoff M, Friston K. On Markov blankets and hierarchical selforganisation. Journal of Theoretical Biology. 2020; 486 110089 [PubMed: 31756340]
- -. Panksepp, J. Oxford University Press; Oxford: 1998.
- -. Pearl, J. Probabilistic Reasoning in Intelligent Systems. Elsevier; San Francisco, CA: 1988.
- -. Penny W, Stephan KE. A dynamic Bayesian model of homeostatic control. Lecture Notes Comput Sci. 2014; 8779 :60–69. DOI: 10.1007/978-3-319-11298-5_7
- -. Pezzulo G. Grounding procedural and declarative knowledge in sensorimotor anticipation. Mind and Language. 2011; 26:78–114.
- -. Pezzulo G, Rigoli F, Friston K. Active Inference, homeostatic regulation and adaptive behavioural control. Prog Neurobiol. 2015; 134 :17–35. [PubMed: 26365173]
- -. Piontelli, A. From fetus to child. Routledge; London: 1992.
- -. Piontelli, A. Twins: From fetus to child. Routledge; London: 2002.
- -. Piontelli, A. Development of Normal Fetal Movements: the First 25 Weeks of Gestation. Springer; Milan: 2010.
- -. Piontelli, A. Development of Normal Fetal Movements: The Last 15 Weeks of Gestation. Springer; Berlin: 2015.
- -. Ramstead MJD, Kirchhoff MD, Constant A, et al. Multiscale integration: beyond internalism and externalism. Synthese. 2019; doi: 10.1007/s11229-019-02115-x
- -. Ramstead MJ, Kirchhoff MD, Friston KJ. A tale of two densities: active inference is enactive inference. Adaptive Behavior. 2019b 1059712319862774
- -. Reddy, V. How infants know minds. Harvard University Press; Cambridge, MA: 2008.
- -. Qin P, Wang M, Northoff G. Linking Bodily, Environmental and Mental States In the Self–A Three-level Model Based on A Meta-analysis. Neuroscience & Biobehavioral Reviews. 2020
- -. Quintero AM, De Jaegher H. Pregnant Agencies: Movement and Participation in Maternal–Fetal Interactions. Frontiers in Psychology. 2020; 11
- -. Rao RP, Ballard DH. Predictive coding in the visual cortex: a functional interpretation of some extra-classical receptive-field effects. Nat Neurosci. 1999 Jan; 2 (1) :79–87. [PubMed: 10195184]
- -. Ratcliffe M. Touch and the sense of reality. The hand: An organ of the mind. 2013 :131–157.
- -. Seth, AK. Open MIND. Metzinger, T, Windt, J, editors. MIND Group; Frankfurt: 2015. 1-24.

- -. Seth AK, Tsakiris M. Being a beast machine: the somatic basis of selfhood. Trends in cognitive sciences. 2018; 22 (11) :969–981. [PubMed: 30224233]
- -. Sheets-Johnstone, M. The primacy of movement. 2nd ed. John Benjamins; New York: 2011.
- -. Sims M. How to count biological minds: symbiosis, the free energy principle, and reciprocal multiscale integration. Synthese. 2020 :1–23. [PubMed: 32989333]
- -. Smith, N. Phenomenology of Pregnancy. Bornemark, J, Smith, N, editors. Södertörn University; Södertörn: 2016.
- -. Smotherman, W, Robinson, S. Developmental Psychobiology and Behavioral Ecology. Blass, EM, editor. Springer; Berlin: 1988. 149–196.
- -. Stephan KE, Manjaly ZM, Mathys CD, Weber LA, Paliwal S, Gard T, Tittgemeyer M, Fleming SM, Haker H, Seth AK, Petzschner FH. Allostatic Self-efficacy: A Metacognitive Theory of Dyshomeostasis-Induced Fatigue and Depression. Front Hum Neurosci. 2016 Nov. 15 (10) :550.
- -. Sterling P. Homeostasis vs allostasis: implications for brain function and mental disorders. JAMA Psychiatry. 2014 Oct; 71 (10) :1192–3. [PubMed: 25103620]
- ten Donkelaar, HJ, Lammens, M, Hori, A, Cremers, CWRJ. Clinical Neuroembryology: Development and Developmental Disorders of the Human Central Nervous system. 2nd Edn. Vol. 1-1. Springer; Berlin: 2014.
- -. Teklenburg G, Salker M, Molokhia M, Lavery S, Trew G, Aojanepong T, et al. Natural selection of human embryos: decidualizing endometrial stromal cells serve as sensors of embryo quality upon implantation. PLoS One. 2010; 5 e10258 [PubMed: 20422011]
- -. Thelen, E, Smith, LB. A Dynamic Systems Approach to the Development of Cognition and Action. MIT Press; Cambridge, MA: 1994.
- -. Thompson, E. Mind in life: Biology, phenomenology, and the sciences of mind. Harvard University Press; London: 2007.
- -. Trevarthen, C. Human growth. 2nd ed. Falkner, F, Tanner, JM, editors. Plenum; New York: 1985. 301–383.
- -. Tsakiris M. My body in the brain: A neurocognitive model of body-ownership. Neuropsychologia. 2010; 48 (3) :703–712. [PubMed: 19819247]
- -. Varela, FJ, Rosch, E, Thompson, E. The Embodied Mind: Cognitive Science and Human Experience. MIT Press; Cambridge, MA: 1991.
- -. Vaughan OR, Fowden AL. Placental metabolism: substrate requirements and the response to stress. Reprod Domest Anim. 2016 Oct; 51 (Suppl 2) :25–35.
- -. von Hofsten C. An action perspective on motor development. Trends in Cognitive Sciences. 2004; 8 :266–272. [PubMed: 15165552]
- -. van der Meer ALH. Keeping the arm in the limelight: Advanced visual control of arm movements in neonates. European Journal of Paediatric Neurology. 1997; 4 :103–108.
- -. Wallace, MJ, Hooper, SB, McDougall, AR. The Lung: Development, Aging and the Environment. Harding, R, Pinkerton, K, editors. Elsevier; Amsterdam: 2015.
- -. Woods HA, Wilson J, An K. information hypothesis for the evolution of homeostasis. Trends Ecol Evol. 2013 May; 28 (5) :283–9. [PubMed: 23182696]
- -. Zahavi, D. Subjectivity and selfhood: Investigating the first-person perspective. MIT Press; Cambridge, MA: 2005.
- -. Young, IM. On Female Body Experience: "Throwing Like a Girl" and Other Essays. Oxford University Press; Oxford: 2005.
- Zoia S, Blason L, D'Ottavio G, Bulgheroni M, Pezzetta E, Scabar A, et al. Evidence of early development of action planning in the human foetus: A kinematic study. Experimental Brain Research. 2007; 176 :217–226. [PubMed: 16858598]