Symmetry-Breaking Dynamics in Development

Phenom Cogn Sci (2017) 16:585–596
DOI 10.1007/s11097-017-9521-3

Noah Moss Brender
noah.mossbrender@concordia.ca

ABSTRACT: Recognition of the *plasticity* of development — from gene expression to neuroplasticity — is increasingly undermining the traditional distinction between structure and function, or anatomy and behavior. At the same time, dynamic systems theory — a set of tools and concepts drawn from the physical sciences — has emerged as a way of describing what Maurice Merleau-Ponty calls the "dynamic anatomy" of the living organism. This article surveys and synthesizes dynamic systems models of development from biology, neuroscience, and psychology in order to propose an integrated account of growth, learning, and behavior. Key to this account is the concept of self-differentiation or *symmetry-breaking*. I argue that development can be understood as a cascade of symmetry-breaking events brought about by the ongoing interactions of multiple, nested, nonlinear dynamic systems whose self-organizing behaviors gradually alter their own anatomical conditions. I begin by introducing the concept of symmetry-breaking as a way of understanding anatomical development. I then extend this approach to motor development by arguing that the organism's behavior grows along with its body, like a new organ. Finally, I argue that the organism's behavior and its world grow together dialectically, each driving the other to become more complex and asymmetrical through its own increasing asymmetry. Thus development turns out to be a form of cognition or sense-making, and cognition a form of development.

KEYWORDS: Dynamic systems, Enactivism, Embodied cognition, Gene expression, Merleau-Ponty, Motor development

Final publication available at:
https://link.springer.com/article/10.1007/s11097-017-9521-3

One of the central theses of the enactive approach in cognitive science is that cognition is a form of life, and life a form of cognition. The standard argument for this thesis draws a parallel between the self-organizing dynamics of the minimal living unity — a single cell — and the sensorimotor neuro-logic of animal behavior (Thompson 2007; Varela 1991). In both cases, the "organizational closure" of the system in question (i.e. its recursive, self-referential, self-organizing structure) gives rise at the same time to a self and to a meaningful world proper to that self. However, the relation between the single cell and the animal with a nervous system is more than merely analogical: the animal is a multicellular organism that begins its life as a single cell. Thus the enactive approach places the phenomenon of *development* center-stage, as the concrete link between minimal cellularity and multicellularity, life and mind, anatomy and cognition. Enactivism calls us to see living organisms as "historical and developmental beings" (Thompson 2007, p. 166), and cognition as a constitutively developmental process.[1]

In taking this developmental approach to cognition, enactivism breaks with the tradition of treating organisms as complex machines that have been "engineered" by evolution, and must be "reverse-engineered" by science (Thompson 2007, pp. 209-211). Looked at *synchronically* — at a single moment in time — there is indeed a striking resemblance between organisms and certain human-made machines: both are composed of a great number of tiny, moving parts, arranged in such a way that they work together harmoniously to accomplish various functions. Thus it is tempting to hypothesize that the movements of the organism, like those of a machine, can be explained by the arrangement of its parts (Descartes 1985/1662; Nicholson 2012). If this arrangement could in turn be explained by the arrangement of base pairs in the organism's genome, then the organism's behavior would be a product of its genes. Thus psychology would ultimately be reducible to physiology, and physiology to genetics.

However, the analogy between organism and machine breaks down when we study the living body *diachronically*, at developmental timescales (Lewontin 1996; Nicholson 2013, 2014). The movements of a machine can be explained by the arrangement of its parts only insofar as this arrangement is *fixed, i.e.* not altered by the machine's own operations. A living body, however, does not have a fixed architecture: its anatomy is constantly being altered by its own activities. At sufficiently short timescales, anatomy can be treated as an invariant causal factor in behavior. At longer timescales, however, we observe that behavior is as much cause as effect of anatomy, slowly altering its own conditions the way a river changes the shape of its bed.

This was one of the key insights of phenomenologist Maurice Merleau-Ponty's first book, *The Structure of Behavior* (1963/1942)[2]:

> [W]hen they are inborn, anatomical structures should be considered as topographical conditions of the original functional development, modifiable by the functioning itself and thus comparable to the electrode which governs the phenomenon of electrolysis but is altered by it in return; when they are acquired, they should be considered the result of the most habitual functioning; thus anatomy should be considered as a cross-section [*coupe*] of physiological development" (p. 38, translation modified).

Merleau-Ponty returned to and deepened these points in his 1957-8 lectures on the concept of Nature by reviewing three scientific studies of the relation between growth and behavior: G. E. Coghill's study of the axolotl salamander in *Anatomy and the*

Problem of Behavior (1929), Arnold Gesell and Catherine Amatruda's study of human development in *The Embryology of Behavior* (1971/1945), and E. S. Russell's *The Directiveness of Organic Activities* (1945).[3] According to Merleau-Ponty (2003), Coghill "shows us that the animal body must be defined dynamically" (p. 145). "[I]f behavior is a mystery for a frozen anatomy, it is because it can be understood only by a dynamic anatomy" (p. 144, translation modified). Indeed, Coghill "shows that the maturation of the organism and the emergence of behavior are one and the same" (p. 144). This point is confirmed by Russell, who "shows that the relations among the cells of a tissue or an organ are assimilable to relations of behavior. Reciprocally, what we call behavior can be considered as a prolongation of the activity of an organism beyond its own body. Behavior is a physiological activity in external circuit. Reciprocally, physiological activity is a behavior facing an internal milieu" (pp. 178-9). For Gesell and Amatruda, similarly, the animal body is "a take [prise] on the exterior world. It follows from this that there is no difference between the organization of the body and behavior" (p. 146). The concepts of *anatomy* and *behavior* thus have a "reciprocal character": "On the one hand, the body is like the envelope, the sketch of behavior; on the other, behavior is literally a second body which is added to the natural body" (p. 147).[4]

Although machine metaphors persist in biology and psychology today, recognition of the *plasticity* of development — from gene expression to neuroplasticity — is increasingly undermining any absolute distinction between structure and function, or anatomy and behavior. At the same time, dynamic systems theory — a set of tools and concepts drawn from the physical sciences — has emerged as a way of describing what Merleau-Ponty calls the "dynamic anatomy" of the living organism.[5] This article will survey and synthesize dynamic systems models of development from biology, neuroscience, and psychology, in order to propose an integrated account of growth, learning, and behavior. Key to this account is the concept of self-differentiation or *symmetry-breaking*.[6] I will argue that development can be understood as a cascade of symmetry-breaking events brought about by the ongoing interactions of multiple, nested, nonlinear dynamic systems whose self-organizing behaviors gradually alter their own anatomical conditions.[7]

I will begin by introducing the concept of symmetry-breaking as a way of understanding anatomical development. I will then extend this approach to motor development by arguing that the organism's behavior grows along with its body, like a new organ. Finally, I will argue that the organism's behavior and its *world* grow together dialectically, each driving the other to become more complex or *asymmetrical*.[8] Thus development turns out to be a form of cognition or sense-making, and cognition a form of development.

1. Symmetry-breaking dynamics in embryogenesis

Every multicellular organism begins its life as a single cell, and grows by repeated cellular reproduction. Cells reproduce by division: the mother cell splits into two daughter cells, which each inherit a copy of their mother's nuclear DNA and half its cytoplasmic contents. Daughter cells are genetically identical to their mother, and to each other. Thus one might expect the repeated division of the spheroid zygote to produce a roughly spheroid mass of identical cells. The puzzle of embryogenesis is to explain how it produces, instead, a highly *asymmetrical* body with a front and a back, a top and a bottom, a left and a right, composed of cells that are highly *differentiated* into a range of specialized tissues and organs (Turvey & Fitzpatrick 1993). “Viewed from the perspective of physics, early development, during which the organism acquires its final shape, is a series of symmetry-breaking events starting from a highly symmetrical spheroidal egg and arriving at a body with a much lower degree of symmetry” (Forgacs & Newman 2005, p. 180). Mathematical models of the processes involved in embryogenesis are increasingly shedding light on how and why these symmetry-breaking events occur. (Mathematicians define symmetry as *invariance under a transformation*: the greater the number of transformations that leave a system unchanged, the higher its degree of symmetry. When a system’s degree of symmetry decreases, the lost symmetries are said to have been “broken,” usually indicating that the system has become less uniform and more differentiated.[9])

Although the cells of a multicellular body are genetically identical, they differ in *which* genes they are capable of expressing, i.e. which segments of their nuclear DNA can be “transcribed” (used as a template for protein synthesis). Whether a given gene can be transcribed, as well as the *rate* of its transcription, is regulated by proteins called “transcription factors,” which work by binding to specific sequences of a cell’s DNA. Transcription factors may be activators, which increase the rate of a gene's transcription, or repressors, which decrease it. However, these transcription factors *are themselves proteins specified by genes and produced by transcription*. Thus the role of DNA in development is characterized by circuits or networks of gene products that mutually regulate one another through positive and negative feedback loops (Forgacs & Newman 2005; E. F. Keller 2000). These *autoregulatory networks* can be modeled as nonlinear dynamic systems: sets of differential equations whose variables represent the changing concentrations of transcription factors within a cell and their rates of change (Forgacs & Newman 2005; A. D. Keller 1995). These systems are called *nonlinear* because gradual changes in one parameter of the system, when they reach a certain *critical point*, generate an abrupt shift in the system's global state — as when gradual accumulation of riverbed sediment causes a river to suddenly overflow its banks and branch off in a new direction.

The developing embryo consists of multiple cells that interact with one another by exchanging transcription factors across cell boundaries, giving rise to a *second-order* autoregulatory network — an autoregulatory network of autoregulatory networks. This second-order network can also be modeled as a nonlinear dynamic system. Kaneko and Yomo (1999) have constructed such a model and used it to simulate the self-differentiation of the growing embryo into different cell types. The simulation begins with a small population of identical cells that can exchange transcription factors with their immediate neighbors and reproduce by division. As the population of model cells grows by cell division, all the cells initially exhibit the same biochemical state (corresponding to a single, shared cell type). However, when the number of cells exceeds a certain critical threshold, this uniform state becomes unstable and the multicellular system undergoes a *symmetry-breaking bifurcation* (an abrupt decrease in the system's degree of symmetry): the population of cells splits into distinct clusters, each exhibiting a different stable biochemical state. These new clusters remain stable as they grow by cell division, with daughter cells inheriting the "cell type" (i.e. the biochemical state) of their parent. As they grow, some clusters undergo new bifurcations, dividing into further clusters with new stable cell states. As in a real body, different types of cell in the model arose through different developmental lineages, which could all be traced back to a single original cell type. These qualitative outcomes were robust under both variations in initial conditions and fluctuations in parameters over time, suggesting that this may be a realistic model of differentiation and development in real multicellular bodies.

In the Kaneko-Yomo model, cells exchange transcription factors only with their immediate neighbors (*juxtacrine signaling*). However, cells in the growing embryo also interact over longer distances (*paracrine signaling*) through the diffusion of transcription factors called *morphogens*. Such global interactions are responsible for macroscopic symmetry-breaking events in development, such as the formation of anterior-posterior and dorsal-ventral body axes in the previously spheroid embryo. These take place through the appearance of “organizers” — self-organizing chemical “hot-spots” that regulate the differentiation of surrounding cells and the orientation of large-scale structures such as the spinal cord (Forgacs & Newman 2005). Meinhardt (2001) has constructed a reaction-diffusion model of organizer-formation as a nonlinear dynamic system. In Meinhardt's model, a slow-diffusing *activator* is positively self-regulating, i.e. it increases its own transcription rate. But this same morphogen also increases the transcription rate of a fast-diffusing *inhibitor,* which negatively regulates transcription of the activator. The result is a self-enhancing feedback loop acting over a short range, which competes with an inhibitory reaction acting over a longer range. Starting from a uniform distribution of the two morphogens, this system will undergo a symmetry-breaking bifurcation in which the activator becomes concentrated in a small “hot spot” surrounded by a cloud of inhibitor. By adding additional morphogens to his model, Meinhardt showed that the formation of one organizer could induce the formation of other organizers at different locations. Thus reaction-diffusion models of this sort may be able to explain the cascade of macroscopic symmetry-breaking events that takes place during embryogenesis.

We began this discussion of embryogenesis with a puzzle: How can a population of genetically uniform cells organize itself into a highly asymmetrical arrangement of diverse cells, tissues, and organs? Solving this puzzle requires a shift of focus from the static structure of the genetic "code" to the dynamic activity or behavior[10] of gene expression,[11] which not only regulates anatomical growth but is also regulated by it. The self-differentiation of the developing embryo can be understood as a cascade of symmetry-breaking events brought about by the ongoing interactions of multiple, nested, autoregulatory transcription networks whose self-organizing activity gradually alters its own anatomical parameters. In the next section, I will extend this perspective from anatomical to motor development.

2. Symmetry-breaking dynamics in motor development

Multicellular organisms arise from the repeated division of one cell into two, and the subsequent differentiation of these once-identical cells into different types, tissues, and organs. Thus growth is a process of *self-articulation* into parts that can oppose one other, pushing one another in different developmental directions. In animals, this process eventually generates a new kind of articulation: the jointed limb. The joint allows the body to oppose itself in a new way, using muscle tension to move one part of itself by pushing off of another. This self-opposition allows the animal body to push off of its surroundings as well, moving across immobile surfaces and manipulating movable objects.

The juxtacrine and paracrine signals discussed above are far too slow to coordinate these gross bodily movements, which are several orders of magnitude larger and faster than the movements of cells within the body. Thus the evolution of mobile, multicellular organisms has been accompanied by the evolution of nerve cells that can communicate rapidly and precisely with one another over short or long distances through specialized axonal and dendritic structures. “Whenever motion is an integral part of the lifestyle of a multicellular, there is a corresponding development of a nervous system linking effector (muscles, secretion) and sensory surfaces (sense organs, nerve endings)” (Varela 1991, p. 89).

Over the course of development, the cells of the nervous system grow into a densely interconnected network. Like the autoregulatory transcription networks discussed above, neural networks can be modeled as nonlinear dynamic systems whose positive and negative feedback loops give rise to complex, emergent dynamics through symmetry-breaking bifurcations or “phase transitions” (Chialvo 2010; Kelso 2012; Sporns 2011; Wilson 1999). The self-organization of short-lived *functional* networks of neural activity slowly alters the more stable *structural* networks that constrain them, by modulating the autoregulatory dynamics of growth and gene expression in the nervous system’s cells (Byrge et al. 2014; Rubinov et al. 2009; Sporns 2011). Thus the anatomy of the nervous system is not fixed, like that of a machine, but *plastic* or *dynamic*: its structure and its activity are interdependent.

The nervous system’s activity is coupled to that of the musculoskeletal system, which can also be modeled as a nonlinear dynamic system with its own complex, self-organizing dynamics (Chiel et al. 2009; Thelen 1995; Thelen & Smith 1994; Zernicke & Schneider 1993). These dynamics are constrained in real time by the biomechanical properties of musculoskeletal anatomy, but also regulate growth and gene expression within muscle, bone, and vascular tissues over longer timescales (Humphrey 2008). Thus musculoskeletal anatomy, like that of the nervous system, is dynamic; and like the nervous system, its structure and its activity are interdependent.

Behavior emerges dynamically from the mutual regulation of these two systems (Beer 2009; Byrge et al. 2014; Chiel and Beer 1997; Chiel et al. 2009; Thelen 1995; Varela 1991). The nervous system regulates the dynamics of the musculoskeletal system by generating muscle contractions, which pump energy into the musculoskeletal system and modulate its biomechanical properties (Chiel et al. 2009). In return, musculoskeletal dynamics regulate brain activity via the body's sense organs. For example, the movements of my head modulate the sensory input I receive through my eyes, ears, nose, and skin.

Just as the autoregulatory networks of gene expression extend beyond the membrane boundaries of the cell, circulating through the other cells that surround it, so too do the autoregulatory dynamics of the nervous system extend beyond the boundaries of the organism, circulating through its environment.[12] "[S]tructural connections are not the only means by which neurons can causally affect the activity of other neurons. Another way in which neural states can cause other neural states is through the environment, as a result of bodily movement that causes changes in sensory inputs" (Sporns 2011, p. 305). Thus behavior acts like another organ or a "second body" (Merleau-Ponty 2003, p. 147) which "extends brain networks into the environment"

(Byrge et al. 2014), connecting different regions of the nervous system via the organism's surroundings.

This "second body" grows in the same way as the first. Just as the anatomy of the adult body is not present from conception, but has to develop over time out of a much simpler, more symmetrical form, so too do the coordinated and adaptive movements of the mature organism have to develop over time from much simpler, more symmetrical behaviors. Studies of motor development in human children suggest that the problem of motor *coordination* (how to move the various parts of the body together effectively) is secondary to the problem of motor *differentiation* (how to move these parts independently of one another). EMG measurements of infant leg movements, for example, show that all the muscles of the newborn's leg — both flexors and extensors — contract together, as if they were a single muscle (Thelen & Fisher 1983). Before the different muscles and joints of the leg can be coordinated effectively, they must first be uncoupled from one another (Thelen 1995). That is, the pattern of muscle activity generated by the infant's nervous system must become more self-differentiated or asymmetrical. New behaviors grow like new organs: the articulation of the growing body into distinct organs and limbs mutually regulates and is regulated by a parallel articulation of *behavior* into increasingly complex and differentiated movements.

Motor development, like embryogenesis, can be viewed as a cascade of symmetry-breaking events brought about by the ongoing interactions of multiple, nested, self-regulating systems whose self-organizing activities (behavior) gradually alter their own parameters (anatomy) (Kelso 2012; Thelen 1995; Thelen & Smith 1994; Turvey & Fitzpatrick 1993). Given the tight coupling between anatomical growth, motor development, and behavior, we might profitably view these not as three distinct processes, but as a single activity observed over longer or shorter timescales.

3. The role of environmental asymmetries in perception and motor development

I have focused so far on the relation between behavior and anatomy. Equally important, however, is the relation between the animal's behavior and its environment. Animal movement evolved as a way of coping with the heterogeneous or asymmetrical distribution of resources (e.g. nutrients, mates) and dangers (e.g. predators, poisons) in the animal's environment. The basic function of the nervous system is to exploit the asymmetry of the environment by using it to regulate the animal's movements (Chialvo 2010; Petitot 1995; Petitot & Smith 1996). I noted above that behavior extends neural networks into the environment via the body's sense organs, and that this is what allows musculoskeletal dynamics to regulate nervous activity. In a perfectly symmetrical or homogeneous environment, however, this external circuit is broken. In a field of uniform illumination, for example, the movements of my eyes produce no corresponding changes in visual input. An environment without *differences* offers nothing to perceive, no responses to the body's questing movements (Merleau-Ponty 2012/1945, p. 4). Thus perception requires an asymmetrical world. Indeed, the more asymmetrical the environment is, the more rich and nuanced will be the sensory feedback it offers to a moving body. This asymmetry is the very *texture* of reality, which allows us to get a perceptual *grip* on our surroundings (Bruineberg & Rietveld 2014; Dreyfus 2002), to "gear into" them with our movements (Merleau-Ponty 2012/1945, p. 261).

Motor development can thus be understood as a process of *coming to grips* with a given environment by learning to exploit its particular asymmetries, to master its "sensorimotor contingencies" (O'Regan & Noë 2001).[13] Studies of humans and animals confirm that the ongoing sensory feedback produced by the organism's own movements is a key driver of motor development (Bourgeois *et al*. 2005; Held & Hein 1963; Needham *et al.* 2002; Palmer 1989; Thelen 1995). In other words, it is the moving body's encounters with differences in its surroundings that drive its own movements to become increasingly differentiated.

At the same time, however, it is the organism's own movements that determine *which* of the available asymmetries in its surroundings the organism actually encounters (Byrge et al. 2014; Kretch et al. 2013; Thelen 1995).[14] "The gaze obtains more or less from things according to the manner in which it interrogates them, in which it glances over them or rests upon them" (Merleau-Ponty 2012/1945, p. 154). As the organism's movements become more articulated and differentiated, they encounter more subtle differences in its surroundings, and these encounters in turn give rise to even more asymmetrical movements (Gibson & Gibson 1955). Thus motor development is driven by a positive feedback loop between movement and perception, or behavior and the situation to which it responds. The organism and its world grow together dialectically, each driving the other to become more complex and differentiated through its own increasing self-differentiation. This is the growth of what enactivists, following Merleau-Ponty, call *sense*: the self-articulating field of differences that make a difference to the organism (Moss Brender 2013).

Conclusion

In this paper, I have argued that the organism's behavior and its world grow in the same way as its body, by division or self-differentiation. Development — including growth, learning, and behavior — can be understood as a cascade of symmetry-breaking events brought about by the ongoing interactions of multiple, nested, nonlinear dynamic systems whose self-organizing behaviors gradually alter their own anatomical and environmental conditions. This process has evolved to be both robust and plastic (Bateson & Gluckman 2011, 2012). If it is too sensitive to internal or external variations, then it will not reliably generate functional and adaptive organs and behaviors. But if it is not sensitive enough, then the organism will be unable to adapt to new situations and environments. Development has no single cause (Johnston & Edwards 2002): the organism inherits from its parents a great deal of structure, including the highly asymmetrical sequence of its DNA; but the organism's development (including the process of differential gene expression) is also shaped by the spatiotemporal asymmetries it encounters in its environment. Some organisms, such as plants, adapt to these asymmetries by having relatively plastic body plans (Trewavas 2003). Since animal locomotion requires a more fixed body plan, developmental plasticity is concentrated in the animal's nervous system. The history of the plant's interactions with its environment is thus visible in the shape of its body, while that of the animal can be seen in its behavior.

If the animal is a reflection of its environment, however, this environment is also a reflection of the animal (Gibson 1986/1979, Lewontin 1991, Merleau-Ponty 1963/1942, 2012/1945). The world teaches the animal how to move, but this world is only revealed to the animal through its own movements. Causality in development is reciprocal or "dialectical" (Merleau-Ponty 1963/1942, p. 160): gene expression regulates anatomy, movement, and perception; but perception equally regulates movement, anatomy, and gene expression. Development is thus the simultaneous growth of body, behavior, and world. This dynamic co-emergence of self and world is what enactivists call *cognition* or *sense-making*. Thus development is a form of cognition, and cognition is a form of development.

REFERENCES

Ball, P. (2009). *Nature's Patterns*, 3 vols. Oxford: Oxford University Press.

Bateson, P., & Gluckman, P. (2011). *Plasticity, Robustness, Development and Evolution*. Cambridge: Cambridge University Press.

Bateson, P., & Gluckman, P. (2012). Plasticity and robustness in development and evolution. *International Journal of Epidemiology, 41*, 219–223

Beer, R. D. (2009). Beyond control: The dynamics of brain-body-environment interaction in motor systems. In D. Sternad (Ed.), *Progress in motor control* (pp. 7-24). New York: Springer.

Bourgeois, K., Khawar, A., & Neal, S. (2005). Infant manual exploration of objects, surfaces, and their interrelations. *Infancy, 8*(3), 233-252.

Bruineberg, J., & Rietveld, E. (2014). Self-organization, free energy minimization, and optimal grip on a field of affordances. *Frontiers in Human Neuroscience*, *8*, 599, doi: 10.3389/fnhum.2014.00599

Byrge, L., Sporns, O., & Smith, L. B. (2014). Developmental process emerges from extended brain–body–behavior networks. *Trends in Cognitive Sciences*, *18*(8), 395-403.

Chialvo, D. R. (2010). Emergent complex neural dynamics. *Nature Physics*, *6*(10), 744-750.

Chiel, H.J. and Beer, R.D. (1997). The brain has a body: adaptive behavior emerges from interactions of nervous system, body and environment. *Trends in Neurosciences* 20, 553–557.

Chiel, H. J., Ting, L. H., Ekeberg, Ö., & Hartmann, M. J. (2009). The brain in its body: motor control and sensing in a biomechanical context. *The Journal of Neuroscience*, *29*(41), 12807-12814.

Coghill, G. E. (1929). *Anatomy and the Problem of Behavior*. New York: Macmillan.

Descartes, R. (1985). *Treatise on Man*. In J. Cottingham, R. Stoothoff, & D. Murdoch (Trans.), *The Philosophical Writings of Descartes*, vol. 1. Cambridge: Cambridge University Press. (Original work published 1662.)

Dreyfus, H. (2002). Intelligence without representation – Merleau-Ponty's critique of mental representation. *Phenomenology and the Cognitive Sciences* 1, 367–383.

Forgacs, G., & Newman, S. A. (2005). *Biological Physics of the Developing Embryo.* Cambridge: Cambridge University Press.

Foti, V. M. (2013). *Tracing Expression in Merleau-Ponty: Aesthetics, Philosophy of Biology, and Ontology*. Evanston, IL: Northwestern University Press.

Gesell, A., & Amatruda, C. S. (1971). *The Embryology of Behavior: The Beginnings of the Human Mind*. Westport, CT: Greenwood Press. (Original work published in 1945.)

Gibson, J. J. (1950). *The Perception of the Visual World*. Cambridge, MA: Riverside Press.

Gibson, J. J. (1965). Constancy and invariance in perception. In G. Kepes (Ed.), *The nature and art of motion* (pp. 60-70). New York: Brazilier.

Gibson, J. J. (1986). *The Ecological Approach to Visual Perception*. New York: Taylor & Francis. (Original work published 1979.)

Gibson, J. J., & Gibson, E. J. (1955). Perceptual learning: differentiation or enrichment? *Psychological review, 62*(1), 32-41.

Hansen, M. B. N. (2004). The Embryology of the (In)visible. In T. Carman & M. B. N. Hansen (Eds.), *The Cambridge Companion to Merleau-Ponty* (pp. 231-264). Cambridge: Cambridge University Press.

Held, R., & Hein, A. (1963). Movement-produced stimulation in the development of visually guided behavior. *Journal of comparative and physiological psychology*, *56*(5), 872-6.

Humphrey, J. D. (2008). Vascular adaptation and mechanical homeostasis at tissue, cellular, and sub-cellular levels. *Cell biochemistry and biophysics*, *50*(2), 53-78.

Johnston, T. D., & Edwards, L. (2002). Genes, Interactions, and the Development of Behavior. *Psychological Review, 109*(1), 26-34.

Kaneko, K., & Yomo, T. (1999). Isologous diversification for robust development of cell society. *Journal of Theoretical Biology*, *199*(3), 243-256.

Keller, A. D. (1995). Model genetic circuits encoding autoregulatory transcription factors. *Journal of Theoretical Biology*, *172*(2), 169-185.

Keller, E. F. (2000). *The Century of the Gene*. Cambridge, MA: Harvard University Press.

Kelso, J. S. (2012). Multistability and metastability: understanding dynamic coordination in the brain. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1591), 906-918.

Kretch, K.S., Franchak, J. M., & Adolph, K. E. (2013) Crawling and walking infants see the world differently. *Child Development*, *85*(4), 1503-1518.

Lee, D., & Aronson, E. (1974). Visual proprioceptive control of standing in human infants. *Perception & Psychophysics*, *15*(3), 529-532.

Lewis, M. D. (2000). The Promise of Dynamic Systems Approaches for an Integrated Account of Human Development. *Child Development*, *71*(1), 36-43.

Lewontin, R. C. (1991). *Biology as Ideology: The Doctrine of DNA*. New York: HarperCollins.

Lewontin, R. C. (1996). Evolution as engineering. In J. Collado-Vides *et al.* (Eds.), *Integrative approaches to molecular biology* (pp. 1-10). Cambridge, MA: MIT Press.

Mainzer, K. (2005). Symmetry and complexity in dynamical systems. *European Review*, *13*(Supp. 2), 29–48.

Marratto, S. L. (2012). *The Intercorporeal Self: Merleau-Ponty on Subjectivity*. Albany, NY: SUNY Press.

Meacham, D. (2014). Sense and life: Merleau-Ponty's philosophy of nature and evolutionary biology. *Discipline Filosofiche*, *24*(2), 137-163.

Meinhardt, H. (2001). Organizer and axes formation as a self-organizing process. *International Journal of Developmental Biology*, *45*(1), 177-188.

Merleau-Ponty, M. (1963). *The Structure of Behavior*. (A. L. Fisher, Trans.). Pittsburgh, PA: Duquesne University Press. (Original work published 1942.)

Merleau-Ponty, M. (2003). *Nature: Course Notes from the Collège de France*. (R. Vallier, Trans.). Evanston, IL: Northwestern University Press.

Merleau-Ponty, M. (2012). *Phenomenology of Perception*. (D. Landes, Trans.). New York: Routledge. (Original work published 1945.)

Morris, D. (2008). The Time and Place of the Organism: Merleau-Ponty's Philosophy in Embryo. *Alter: Revue de phénoménologie*, *16*, 69-86.

Morris, D. (2012). Merleau-Ponty, Passivity and Science: From Structure, Sense and Expression, to Life as Phenomenal Field, via the Regulatory Genome. *Chiasmi International: Trilingual Studies Concerning Merleau-Ponty's Thought*, *14*, 89-111.

Moss, L. (1992). A kernel of truth? On the reality of the genetic program. *Proceedings of the Biennial Meeting of the Philosophy of Science Association*, *1992*(1), 335-348.

Moss Brender, N. (2013). "Sense-Making and Symmetry-Breaking: Merleau-Ponty, Cognitive Science, and Dynamic Systems Theory." *Symposium: Canadian Journal of Continental Philosophy*, *17*(2), 247-271.

Needham, A., Barrett, T., & Peterman, K. (2002). A pick-me-up for infants' exploratory skills: Early simulated experiences reaching for objects using 'sticky mittens' enhances young infants' object exploration skills. *Infant Behavior and Development*, *25*, 279-295.

Nicholson, D. J. (2012). The concept of mechanism in biology. *Studies in History and Philosophy of Biological and Biomedical Sciences*, *43*, 152-163.

Nicholson, D. J. (2013). Organisms ≠ Machines. *Studies in History and Philosophy of Biological and Biomedical Sciences*, *44*(4), 669-678.

Nicholson, D. J. (2014). The machine conception of the organism in development and evolution: A critical analysis. *Studies in History and Philosophy of Biological and Biomedical Sciences*, *48*, 162-174.

Norton, A. (1995) Dynamics: An Introduction. In R. F. Port & T. van Gelder (Eds.), *Mind as Motion: Explorations in the Dynamics of Cognition*. Cambridge, MA: MIT Press.

Oyama, S. (2000). *The Ontogeny of Information*, 2nd Ed. Durham, NC: Duke University Press.

O'Regan, J. K., & Noë, A. (2001). A sensorimotor account of vision and visual consciousness. *Behavioral and Brain Sciences*, *24*(5), 939-1031.

Palmer, C. (1989). The discriminating nature of infants' exploratory actions. *Developmental Psychology*, *25*(6), 885-893.

Petitot, J. (1995). Morphodynamics and attractor syntax: constituency in visual perception and cognitive grammar. In R. F. Port & T. van Gelder (Eds.), *Mind as Motion: Explorations in the Dynamics of Cognition*. Cambridge, MA: MIT Press.

Petitot, J., & Smith, B. (1996). Physics and the Phenomenal World. In R. Poli and P. M. Simons (Eds.), *Formal Ontology* (pp. 233-253). Dordrecht: Springer.

Pollard, C. (2014). Merleau-Ponty and Embodied Cognitive Science. *Discipline Filosofiche*, *24*(2), 67-90.

Robert, J. S. (2004). *Embryology, Epigenesis, and Evolution: Taking Development Seriously*. Cambridge: Cambridge University Press.

Rouse, J. Merleau-Ponty's Existential Conception of Science. In T. Carman & M. B. N. Hansen (Eds.), *The Cambridge Companion to Merleau-Ponty* (pp. 265-290). Cambridge: Cambridge University Press.

Rubinov, M., Sporns, O., van Leeuwen, C., & Breakspear, M. (2009). Symbiotic relationship between brain structure and dynamics. *BMC neuroscience*, *10*(1), 55.

Russell, E. S. (1945). *The Directiveness of Organic Activities*. Cambridge: Cambridge University Press.

Russon, J. (2003). *Human Experience: Philosophy, Neurosis, and the Elements of Everyday Life*. Albany, NY: SUNY Press.

Schmidt, J. C. (2008). From Symmetry to Complexity: On Instabilities and the Unity in Diversity in Nonlinear Science. *International Journal of Bifurcation and Chaos*, *18*(4), 897-910.

Sporns, O. (2011). *Networks of the Brain*. Cambridge, MA: MIT Press.

Stewart, I., & Golubitsky, M. (1992). *Fearful Symmetry: Is God a Geometer?* Oxford: Blackwell.

Strogatz, S. H. (2001). *Nonlinear Dynamics and Chaos: With Applications to Physics, Biology, Chemistry, and Engineering*. Cambridge, MA: Westview Press.

Thelen, E. (1995). Motor development: A new synthesis. *The American Psychologist*, *50*(2), 79-95.

Thelen, E., & Fisher, D. M. (1983) The Organization of Spontaneous Leg Movements in Newborn Infants. *Journal of Motor Behavior 15*(4), 353-372.

Thelen, E., & Smith, L. (1994). *A Dynamic Systems Approach to the Development of Cognition and Action*. Cambridge, MA: MIT Press.

Thompson, E. (2007). *Mind in Life*. Cambridge, MA: Harvard University Press.

Toadvine, T. (2009). *Merleau-Ponty's Philosophy of Nature*. Evanston, IL: Northwestern University Press.

Trewavas, A. (2003). Aspects of Plant Intelligence. *Annals of Botany*, *92*, 1-20.

Turvey, M. T., & Fitzpatrick, P. (1993). Commentary: Development of Perception-Action Systems and General Principles of Pattern Formation. *Child Development*, *64*(4), 1175-1190.

van Gelder, T. (1995). What Might Cognition Be, If Not Computation? *The Journal of Philosophy, 92*(7), 345-381.

van Gelder, T. (1998). The Dynamical Hypothesis in Cognitive Science. *Behavioral and Brain Sciences*, *21*(5), 615-665.

van Gelder, T., & Port, R. F. (1995). It's About Time: An Overview of the Dynamical Approach to Cognition. In R. F. Port & T. van Gelder (Eds.), *Mind as Motion: Explorations in the Dynamics of Cognition*. Cambridge, MA: MIT Press.

Varela, F. J. (1991). Organism: A Meshwork of Selfless Selves. In A. I. Tauber (Ed.), *Organism and the Origins of Self*. Dordrecht: Kluwer.

Welsh, T. (2006). From Gestalt to Structure: Maurice Merleau-Ponty's Early Analysis of the Human Sciences. *Theory & Psychology*, *16*(4), 527-551.

Wilson, H. R. (1999). *Spikes, decisions, and actions: The dynamical foundations of neuroscience*, vol. 5. Oxford: Oxford University Press.

Zernicke, R. F., & Schneider, K. (1993). Biomechanics and developmental neuromotor control. *Child development*, *64*(4), 982-1004.

---

[1] Multicellular organisms also *evolved* from single-celled organisms. Thus the enactive approach also emphasizes the evolved character of both cognition and development (Thompson 2007). However, this article focuses not on evolution, but on development, which is many orders of magnitude faster and thus much easier to observe directly.

[2] For more on the relation between Merleau-Ponty and enactivism, including criticism in

[2] For more on the relation between Merleau-Ponty and enactivism, including criticism in both directions, see Dreyfus 2002, Marratto 2012, Moss Brender 2013, Pollard 2014, Thompson 2007.

[3] On Merleau-Ponty's method of using scientific sources for philosophical purposes, see Meacham 2014, Morris 2012, Rouse 2004, Toadvine 2009, Welsh 2006. My own use of

---

empirical research is informed both by Merleau-Ponty's method and by his results, which this article attempts to revise and build upon using more recent science.

[4] For more on Merleau-Ponty's discussion of embryology and development in the *Nature* lectures, see Foti 2013, Hansen 2005, Morris 2008.

[5] For introductions to dynamic systems theory, see Norton 1995, Strogatz 2001.

[6] This focus on symmetry-breaking distinguishes my account from those of Johnston & Edwards (2002) and Lewis (2000), but I take the three accounts to be compatible and complementary.

[7] The role of symmetry-breaking in my account might usefully be compared to the role played by *programs* or *algorithms* in mechanistic accounts of development, but I lack the space to do this here. For criticism of the concept of "programs" in biology, see E. F. Keller 2000, Moss 1992, Oyama 2000, Robert 2004; and in the cognitive sciences, see Thelen & Smith 1994, van Gelder & Port 1995, van Gelder 1995, 1998.

[8] For more on the epistemological and ontological implications of these claims, and their relation to Merleau-Ponty's concept of *form* (Gestalt), see Moss Brender 2013.

[9] For introductions to symmetry and symmetry-breaking, see Ball 2009, Mainzer 2005, Schmidt 2008, Stewart & Golubitsky 1992.

[10] Recall Merleau-Ponty's claim that "physiological activity is a behavior facing an internal milieu" (2003, p. 179).

[11] See E. F. Keller 2000 on the current shift from *structural* to *functional* genomics (p. 7).

[12] Recall Merleau-Ponty's claim that behavior "can be considered as a prolongation of the activity of an organism beyond its own body," or "a physiological activity in external circuit" (2003, pp. 178-9)

---

[13] This mastery is equally a dependence and a vulnerability. Sensorimotor habits acquired in one environment can become a liability in novel environments, as demonstrated by the "moving room" experiments of Lee and Aronson (1974). Russon (2003) argues that this is the structure of human neurosis: embodied habits acquired in one context propel us into new situations to which these habits are no longer adequate.

[14] Recall the definition of symmetry as *invariance under a transformation*. We can think of the organism's movements as transformations that reveal environmental (a)symmetries by generating variations and invariants in the organism's perceptual field (Gibson 1950, 1965, 1986/1979). Which environmental (a)symmetries the organism discovers will thus depend on which transformations it applies (Moss Brender 2013).