



Review article

Affordances and neuroscience: Steps towards a successful marriage

Matthieu M. de Wit^{a,*}, Simon de Vries^b, John van der Kamp^c, Rob Withagen^b^a Department of Neuroscience, Muhlenberg College, USA^b Center for Human Movement Sciences, University of Groningen, University Medical Center Groningen, The Netherlands^c Institute of Brain and Behaviour Amsterdam, Faculty of Behavioural and Movement Sciences, Vrije Universiteit, Amsterdam, The Netherlands

ARTICLE INFO

Keywords:

Affordance
 Standard cognitive neuroscience
 Subject-object framework
 Gibson
 Perceptual system
 Action system
 Degeneracy
 Neural reuse
 Functional connectivity

ABSTRACT

The concept of affordance is rapidly gaining popularity in neuroscientific accounts of perception and action. This concept was introduced by James Gibson to refer to the action possibilities of the environment. By contrast, standard cognitive neuroscience typically uses the concept to refer to (action-oriented) representations in the brain. This paper will show that the view of affordances as representations firmly places the concept in the subject-object framework that dominates both psychology and neuroscience. Notably, Gibson introduced the affordance concept to overcome this very framework. We describe an account of the role of the brain in perception and action that is consistent with Gibson. Making use of neuroscientific findings of neural reuse, degeneracy and functional connectivity, we conceptualize neural regions in the brain as dispositional parts of perceptual and action systems that temporarily assemble to enable animals to directly perceive and – in the paradigmatic case – utilize the affordances of the environment.

Although the term originates in ecological psychology, affordances are now commonly discussed in the cognitive neuroscience literature (as here) without any strict adherence to Gibson's broader theoretical position. (Makris et al., 2013, p. 797)

1. Introduction

Over the last two decades, an increasing number of cognitive neuroscientists has adopted the concept of affordance in their attempts to understand the role of the brain in action and the perception of (higher-order properties of) manipulable objects such as tools (e.g., Bach et al., 2014; Buccino et al., 2009; Cisek, 2007; Evans et al., 2016; Fagg and Arbib, 1998; Jeannerod, 1994; Kühn et al., 2014; Makris et al., 2013; Proverbio et al., 2013; Sakreida et al., 2016; Valyear et al., 2012). The ecological psychologist James Gibson originally introduced this concept to refer to the action possibilities of the environment that are available to an animal. For example, for most human-beings a chair affords sitting, a glass affords grasping, water affords drinking, and the floor affords walking across. However, when using the concept of affordance, cognitive neuroscientists typically do not refer to the action possibilities of the environment, but instead refer to (action-oriented) representations or dispositions in the brain (see e.g., Sakreida et al., 2016). In the present paper, we first show how this approach both fails to do justice to as well as exploit the power of Gibson's theoretical framework, and

then sketch in bold strokes what a genuine Gibsonian neuroscience would look like.

We will start with a discussion of three influential neuroscientific accounts in which the concept of affordance is used, and transformed. We will then elaborate on how Gibson introduced the term affordance to overcome the subject-object framework that dominated psychology, and on how standard cognitive neuroscience, with its central reliance on representation and computation, firmly places the affordance concept back within this subject-object framework (see also Dotov et al., 2012). Capitalizing on Gibson's (1966) theory of perceptual systems, Anderson's (2014) recent theory of neural reuse, and reports of degeneracy in the brain (e.g., Noppeney et al., 2004), we will end with a discussion of a neuroscientific account of affordances that does do justice to Gibson's theoretical framework. It will be argued that brain regions are *parts* of perceptual and action systems that provide animals with the capacity to directly perceive and utilize affordances.

2. Affordances in standard cognitive neuroscience

The concept of affordance is often used in neuroscientific accounts, and not always incorrectly (see e.g., Anderson, 2014; Bruineberg and Rietveld, 2014; Reed, 1996). However, in this section we will limit ourselves to influential accounts, exemplary of standard cognitive neuroscience, that use the concept of affordance in ways that are not in

* Corresponding author.

E-mail address: matthieudewit@muhlenberg.edu (M.M. de Wit).

line with the traditional Gibsonian notion.¹ Specifically, we will focus on the FARS (Fagg-Arbib-Rizzolatti-Sakata) model (Fagg and Arbib, 1998), Tucker and Ellis' (1998) affordance effect, and Cisek's (2007) affordance competition hypothesis.

2.1. The FARS model (Fagg, Arbib, Rizzolatti, and Sakata)

Fagg and Arbib (1998) developed a computational model of the cortical control of grasping. Their goal with this model, which they termed the FARS model, was to provide cognitive neuroscience with “[...] an antidote to an overly exclusive focus on object recognition as the goal of human processing” (p. 1277). Indeed, they aimed to shift focus toward the functional significance of objects. Fittingly, they adopted the concept of affordance, but defined it as follows:

Gibson used the term *affordances* to mean parameters for motor interaction that are signaled by sensory cues without invocation of high-level object recognition processes. (Fagg and Arbib, 1998, p. 1277, emphasis in original)

In this interpretation, affordances are conceptualized as neural transformations of visual cues into grasps. These transformations are hypothesized to occur in a neural network involving the anterior intraparietal area (AIP), area F5 of premotor cortex, and inferotemporal cortex (Fagg and Arbib, 1998). Although they attribute their definition of affordances to Gibson, Fagg and Arbib appear to a certain extent aware of the incongruence between their interpretation and Gibson's use of the term: “[...] unlike Gibson, we imagine several intervening levels of processing between the retina and the extraction of affordances.” (p. 1278). However, this is the only discrepancy Fagg and Arbib identify, and, importantly, one that does not mention the mutuality of the agent and the environment that is central to Gibson's conception of affordances (see below, Section 3.1).

2.2. The affordance effect (Tucker and Ellis)

In a series of behavioral experiments, Tucker and Ellis showed that actions may be potentiated after seeing an image of an object which affords these actions (Ellis and Tucker, 2000; Symes et al., 2007; Tucker and Ellis, 2004, 2001, 1998). Specifically, in their seminal study Tucker and Ellis (1998) showed participants images of common graspable objects and asked them to categorize these images as either upright or inverted by pressing a button as quickly as possible with either their left or their right hand. When the object was oriented to the right and would therefore be easiest to grasp with the right hand, reaction times (RT) for the right hand were shorter than those for the left hand, and vice versa. The authors concluded that merely seeing an object can potentiate actions that are associated with the object and coined this potentiation the ‘affordance effect’. In explaining their findings, Tucker and Ellis used the following definition of affordances:

We use the term *affordance* to refer to the motor patterns whose representations visual objects and their properties give rise to, both during explicit goal-directed acts [...] as well as, we argue, before explicit intentions have been formed. (Tucker and Ellis, 1998, p. 833, emphasis in original)

Later, Ellis and Tucker (2000) describe the effects of seen objects on RT as “micro-affordances, which are said to be dispositional [*sic*] states of the viewer's nervous system” (p. 451). They are aware that their interpretation of affordances as representations deviates from Gibson.

In contrast to this [Gibsonian] notion of affordances being dispositional properties of objects and events, our notion has them as dispositional properties of a viewer's nervous system. (Ellis and Tucker,

2000, p. 466)

Although the initial studies by Tucker and Ellis were behavioral and did not involve measurements of brain activity, the above quote shows that they took their results to inform the way action relevant features of objects are represented in the brain. Later papers studying the neural correlates of the ‘affordance effect’ followed their representational definition of affordances (e.g., Grèzes and Decety, 2002; see also Creem-Regehr and Lee, 2005). Statements such as: “the parietal cortex provides affordance information” (Grèzes and Decety, 2002, p. 213) are clearly reminiscent of an interpretation of affordances along the lines of Tucker and Ellis (see Proctor and Miles, 2014 for further critique).

2.3. The affordance competition hypothesis (Cisek)

The final transformation of the affordance concept in neuroscience that will be discussed here is Cisek's ‘affordance competition hypothesis’ (Cisek, 2007; Cisek and Kalaska, 2010; Cisek and Pastor-Bernier, 2014; Pezzulo and Cisek, 2016). This account starts from the assumption that the brain has evolved to enable organisms to interact with their environment in adaptive ways. It is proposed that during the selection and specification of actions, the brain does not process information serially, but rather in a parallel manner, leading to representations that combine sensory, motor and cognitive elements.

[S]ensory information arriving from the world is continuously used to specify several currently available potential actions, while other kinds of information are collected to select from among these the one that will be released into overt execution at a given moment. [...] From this perspective, behavior is viewed as a constant competition between internal representations of the potential actions which Gibson (1979) termed ‘affordances’. (Cisek, 2007, p. 1586)

Cisek's (2007) model incorporates regions in each of the four lobes of the cortex, as well as the basal ganglia and cerebellum, with the competition between affordances playing out in particular in reciprocal connections within fronto-parietal regions (see Cisek, 2007, Fig. 1). As we will explore in more depth below, Cisek's notion of behavior as continuous interaction and adaptation to a changing environment fits well with the ecological approach. However, his interpretation of affordances as representations of potential actions obviously does not, even if these representations are non-modular (e.g., Fuster, 2000) and their functional role is “[...] not to describe the world [in action-neutral terms], but to mediate adaptive interaction with the world” (Cisek, 2007, p. 1594).²

A shared – and defining – characteristic of the three accounts described above is their depiction of the concept of affordance as a neural representation of motor patterns for actions that are afforded to the observer. Declerck (2013) terms this approach the simulation theory of affordance perception (STAP) and traces its initial formulation to Jeannerod (2001, 1994; Jeannerod et al., 1995). STAP proposes that affordance perception is subserved by motor simulation mechanisms, which not only “[...] shape the motor system in anticipation to execution, but also [...] provide the self with information on the feasibility and the meaning of potential actions” (Jeannerod, 2001, p. S103). Thus, “[d]uring object-directed action, a pragmatic representation is activated in which object affordances are transformed into specific motor schemas [...]” (Jeannerod, 1994, p. 187). It is clear that within several influential neuroscientific accounts, affordances are representational concepts that are decidedly placed *inside* the brain (and waiting to be activated).

¹ For an excellent treatment of how Gibson's ecological approach is misrepresented in textbooks see Costall and Morris (2015).

² In later work (e.g., Cisek and Kalaska, 2010), Cisek no longer defines affordances as representations of potential actions, but instead follows Gibson by defining them as the action possibilities of the environment.

3. Gibson's ecological program

The above discussions of the role of the brain in action selection and grasping emphasize that perception and action representations are intimately linked, and perhaps not even separable in a meaningful way (e.g., Cisek, 2007). However, in developing his ecological approach, Gibson's intention was not simply to couple perception and action, but to overcome the subject-object framework that had dominated psychology from the mechanization of the worldview onwards.

In the 17th century, Galileo and Newton, among others, developed the idea that we can understand the inanimate world as a machine (Dijksterhuis, 1950). It consists exclusively of matter in motion and is completely governed by the laws of mechanics. Although this mechanistic approach was very successful when it came to physics, it was problematic for the human sciences—it made psychology dualistic from the very start (e.g., Costall, 1995; Reed, 1996).

[Modern science] substituted for our world of quality and sense perception, the world in which we live, and love, and die, another world—the world of quantity, of reified geometry, a world in which, though there is a place for everything, there is no place for man. (Koyré, 1965, p. 24; quoted in Costall, 1995)

The mechanization of the worldview implies that there are two worlds. On the one hand, there is the *objective* world, consisting solely of matter in motion. On the other hand, there is the *subjective* world, the world as we experience it, permeated with meaning, perceived colors, tastes, smells, and so on (Reed, 1996). Within this framework, thinkers like Descartes, Kant, Müller, and Helmholtz developed their theories of perception. And although these theories differ from each other to quite some extent, they all adhere to the two-world-assumption, in which there is an environment as described by physics and a perceived environment, the former being considered the *real* environment. Consequently, the theories entail that perception is fundamentally representational—the experienced environment is a product of mental processes that mediate the contact between the perceiver and the real environment.

More recent traditional cognitive neuroscientific accounts follow a similar line of reasoning (e.g., Kanwisher, 2010). Indeed, they typically hold that one of the main functions of the visual brain is to form action-neutral perceptual representations of the world. These representations can subsequently be used to plan an action and to instruct the body. Although, by contrast, the above-described neuroscientific accounts (Cisek, 2007; Fagg and Arbib, 1998; Tucker and Ellis, 1998) argue that perception and action are intimately coupled (i.e., we perceive the environment in action relevant terms), they still adhere to the assumptions of the brain as the commander of the body and perception as being representational (referring to the representations as affordances). As we will explain over the next three sections, it is these very assumptions that Gibson aimed to overcome.

3.1. The affordance concept and its significance

Gibson's ecological approach can be understood as one big critique on mechanistic psychology (e.g., Costall, 1995; Reed, 1996; van Dijk and Withagen, 2014; Withagen and Michaels, 2005). Among other things, Gibson criticized the above physicalist description of the environment that many psychologists adopted.

According to classical physics, the universe consists of bodies in space. We are tempted to assume, therefore, that we live in a physical world consisting of bodies in space and that what we perceive consists of objects in space. But this is very dubious. (Gibson, 1979/1986, p. 16)

According to Gibson, animals do not live in a world consisting of matter in motion, but in an environment consisting of affordances. Although he introduced the affordance concept in the mid 1960s (1966,

p. 285), he came up with a sketchy definition only in the late 1970s, most famously in Chapter 8 of his last book *The ecological approach to visual perception* (1979/1986).

The *affordances* of the environment are what it *offers* the animal, what it *provides* or *furnishes*, either for good or ill. (Gibson, 1979/1986, p. 127; emphases in original)³

As mentioned, for human-beings, a chair affords sitting, a cup affords grasping, water affords drinking, the floor affords walking across, and so on. Note that affordances exist by virtue of a *relationship* between the animal's action capabilities and its environment. As an example, it is the size of the cup relative to the span of a person's hand that determines whether it is graspable, and the slope and rigidity of the floor in combination with the person's walking ability that determines whether it is traversable. After defining affordances, Gibson (1979/1986) was quick to emphasize this revolutionary aspect of his concept: "I mean by [affordances] something that *refers to both the environment and the animal* in a way that no existing term does. It implies the complementarity of the animal and the environment" (p. 127, emphasis added).

Hence, an environment consisting of affordances is not an objective one in which we are not at home, as the mechanistic worldview implied; rather, it is an animal-relative environment and thus "includes us" (Costall, 1999; see also Costall, 2004). Indeed, the concept of affordances does away with the subject-object framework that has held psychology captive for centuries.

An affordance is neither an objective property nor a subjective property; or it is both if you like. An affordance cuts across the dichotomy of subjective-objective and helps us to understand its in-adequacy. It is equally a fact of the environment and a fact of behavior. It is both physical and psychological, yet neither. An affordance points both ways, to the environment and to the observer. (Gibson, 1979/1986, p.129)

Thus, an environment consisting of affordances is a meaningful environment. The affordances of the animal's environment determine what the animal can do in it, what the environment means to the animal. Hence, meaning is not a property that is attached to meaningless sensory stimulation in perceptual processes; rather, it emerges in the animal-environment relationship and can be discovered by the animal during processes of learning. As Gibson put it,

The world of physical reality does not consist of meaningful things. The world of ecological reality, as I have been trying to describe it, does. If what we perceived were the entities of physics and mathematics, meanings would have to be imposed on them. But if what we perceive are the entities of environmental science, their meanings can be *discovered*. (Gibson, 1979/1986, p. 33; emphasis in original)

3.2. The perception and utilization of affordances

The subject-object distinction is also absent in Gibson's theory of direct perception. In his view, perception is not a process in which a neural representation of the environment is formed; rather, perception is a process of being-in-touch with the affordances of the environment.

³ Following its introduction by Gibson, the ontological status of the affordance concept has received much debate. For example, some authors (e.g., Chemero, 2003) conceptualize affordances as properties of the relationship between animals and their environments, while others (e.g., Turvey, 1992) conceptualize affordances as dispositional properties of the environment. However, as we explain here, Gibson introduced the concept to overcome the subject-object framework and hence most commonly stresses its relational character in his writings. While important and substantial development of the affordance concept has taken place within the greater ecological community over the last few decades, for the purpose of the present paper, we limit ourselves to an elaboration of Gibson's original definition of the concept.

To explain this process, Gibson developed an ecological optics. He claimed that the patterns in the ambient energy array (i.e., the totality of the available stimulus energy that surrounds us) provide a specification of the environment and our relationship with it. That is, patterns in the array typically relate one-to-one to the affordances of an animal's environment. Gibson stressed that different energy patterns can provide the same information. For example, not only optical energy, but also acoustical, chemical and radiant energy can specify the presence of a fire and what it affords (Gibson, 1966, p. 54–55). Perception, then, is the process by which animals “resonate” to this information, and by doing so they are in direct perceptual contact with an animal-relative environment.

To perceive the world is to coperceive oneself. This is wholly inconsistent with dualism in any form, either mind-matter dualism or mind-body dualism. The awareness of the world and of one's complementary relations to the world are not separable. (Gibson, 1979/1986, p. 141)

Moreover, information not only allows animals to directly perceive what the environment affords to them, it can also guide the actualization or utilization of affordances. In the late 1950s, Gibson (1958) claimed that by moving through the environment, the animal creates an optic flow field in the ambient energy array that can be used by the animal for the guidance of its motor behavior.

3.3. Empirical research inspired by Gibson's framework

Over the last decades, a large body of empirical research in ecological psychology has focused on the question of whether (human) animals are indeed able to directly perceive and utilize affordances. In contrast with the neuroscientific work described above (Cisek, 2007; Fagg and Arbib, 1998; Tucker and Ellis, 1998), these studies do not conceptualize affordances as neural representations but rather follow Gibson in treating them as properties of the animal-environment relationship. Adolph et al. (1993), for example, studied toddlers' perception of the traversability of sloped surfaces. Fourteen-month-olds were found to accurately match their locomotor strategies to the specific affordances available to them. There was a close relationship between the steepness of the walked-upon slope and toddlers' walking experience, walking skills, and the degree to which they had a more adult-like body morphology. In case of a perceived inability to traverse the slope by walking, toddlers would either refuse, take a detour, or slide down (having perceived the slope to be slide-down-able). In his classic study, Warren (1984) demonstrated that human-beings are capable of accurately perceiving both the maximum staircase riser height that they can climb, and their individual energetically optimal riser height. More specifically, observers perceived risers that were equal to or lower than 0.88 their leg length and 0.26 times their leg length, to be step-on-able and energetically optimal, respectively. Mark (1987), studying sit-on-ability, found that after a brief amount of practice participants could accurately judge their new maximum sitting height when wearing 10 cm blocks attached to the feet. Notably, participants inaccurately estimated the height in cm of the blocks themselves. Zhu and Bingham (2011) reported similar evidence for accurate affordance perception on the one hand, and inaccurate perception of properties of the environment described in physicalist terms, on the other. When asked to judge both the weight and maximum throwability of spherical objects that varied in mass and/or size, participants were subject to the size-weight ‘illusion’ (i.e., when two objects are of equal mass but different size, the larger is perceived as lighter). Their throwability judgments, however, reflected accurate perception of maximum throwability.

Perception of throwability evidently depends not only on the to-be-thrown object, but also on participants' skill or capability to throw, arguably more so than on their particular body morphologies (cf. sit-on-ability). Fajen (2005a,b) has focused explicitly on such action-scaled

affordances. His studies suggest that during the ongoing guidance of braking, drivers are exquisitely sensitive to the limits of the car's braking capabilities. When the deceleration required to stop near a target is well below the maximum deceleration of the brake, braking behavior is variable, with participants performing the task in multiple ways. However, when the required deceleration approaches the maximum deceleration capacity, participants almost always increase their brake pressure. Thus, during deceleration participants continuously take into account their braking capabilities, which shows that agents can indeed perceive affordances that are constrained by their action capabilities. Similar results have been observed in fly ball catching. Judgments of catchability closely correspond to actual catchability as determined by individual outfielders' capabilities (Oudejans et al., 1996).

In addition to addressing whether human-beings are capable of perceiving and utilizing affordances, ecological psychologists have also studied whether they are able to do so directly, on the basis of information. Chapman (1968) argued that agents can perceive whether a fly ball will land in front or behind them on the basis of the optical acceleration of the ball. Human-beings are able to detect this information in multiple ways, in which different anatomical structures are involved. For example, the perceiver may fixate a stationary point in the environment, resulting in the ball giving rise to a retinal flow. However, the perceiver might also follow the ball with the eyes, or keep the eyes relatively motionless in the head and track the ball with the head. Studies have shown that perceivers can indeed detect optical acceleration in each of these three ways (e.g., Bongers and Michaels, 2008; for similar examples in the field of dynamic touch, see Carello et al., 1992; de Vries et al., 2015; Pagano et al., 1993; Withagen and Michaels, 2004).

A number of conclusions can be drawn from the empirical study of affordances—properly construed. First, animals indeed appear to perceive the world in animal-relative terms; animals are sensitive to what they can do with their environment both as determined by their body dimensions and action capabilities (e.g., Adolph et al., 1993; Fajen, 2005a,b; Franchak et al., 2010; Mon-Williams and Bingham, 2011; Oudejans et al., 1996; Warren, 1984). By contrast, they are strikingly inaccurate when asked to describe the world in physicalist terms (e.g., Mark, 1987; Zhu and Bingham, 2011). Second, there is evidence that information in the ambient energy array is used to perceive and utilize affordances (e.g., Michaels et al., 2001; Solomon and Turvey, 1988; Tresilian, 1999; van Hof et al., 2008; Warren et al., 2001). Third, and most importantly for our present purposes, agents show a tendency to utilize affordances in multiple ways (e.g., Bongers and Michaels, 2008; Carello et al., 1992; Fajen, 2005a). As we will see in the next section, Gibson's theoretical framework explicitly predicts this multiple realizability of function, both in the body and the brain.

4. What does a Gibsonian neuroscience look like?

Gibson's theories of affordances and of information led him to a different view of the role of the brain in perceiving and acting. Since the late 17th century the brain has been thought of as the control system of the body (e.g., Martensen, 2004; Zimmer, 2004). However, if action is guided by information, the brain should no longer be conceived as an organ that controls the body. As Gibson put it, “[l]ocomotion and manipulation [...] are controlled not by the brain, but by information [...]. Control lies in the animal-environment system” (Gibson, 1979/1986, p. 225). This is not to deny that the brain is crucially involved in perception and action; rather it implies that the brain is only one of several constituents and that the role of the brain in these processes should be reconsidered.

Ecological psychology has been criticized for not developing a neural account of perception and action. Dennett (1998), for example, accused Gibsonians for treating the brain as “wonder tissue, resonating with marvelous sensitivity to a host of sophisticated affordances” (p.

204). However, a number of theorists have developed ecological approaches to the brain (e.g., Anderson, 2014; Bruineberg and Rietveld, 2014; Reed, 1996; and see e.g., van der Meer et al., 2013 for empirical work). Moreover, Gibson made several claims about the brain that can provide an entry point for the development of an ecological or Gibsonian neuroscience, one that is grounded in his concepts of affordances and direct perception (de Wit et al., 2016).

An important claim that Gibson made about the brain is that it is only a part of what he referred to as *perceptual systems*.

We are told that vision depends on the eye, which is connected to the brain. I shall suggest that natural vision depends on the eyes in the head on a body supported by the ground, the brain being only the central organ of a complete visual system. (Gibson, 1979/1986, p. 1)

Perceiving is not something that occurs simply in a brain connected to a set of sensors. Rather, many parts of the body are involved in actively exploring the richly structured ambient energy array. Indeed, according to Gibson's theory of perceptual systems, anatomical structures temporarily assemble in the process of the detection of information for affordances (see also Bingham, 1988; Kugler and Turvey, 1987). Moreover, Gibson took a functionalist approach to understanding the organization of the brain and body during perception and action. In *The senses considered as perceptual systems*, Gibson (1966) emphasized that the same affordance can be perceived in different ways, involving different pieces of anatomy. Drawing heavily upon Walls' (1942) seminal book on the evolution of the vertebrate eye, Gibson (1966) argued that animals with anatomically different eyes (compound eyes or chambered ones) can detect the same informational patterns in optic flow fields. However, he claimed that this multiple realizability of function is not only present between animals but also within an animal. As mentioned above, Bongers and Michaels (2008) demonstrated that the same perceptual function can indeed be established by different temporarily assembled anatomical structures that are suitable to the task. Notably, this phenomenon has also been observed in neuropsychology and neuroscience (different neuroanatomical structures can support the same function), where it is referred to as degeneracy (Noppeney et al., 2004; Price and Friston, 2002; Sporns, 2011).

Gibson stressed that in addition to the fact that realization of the same function can involve different pieces of anatomy, the same piece of anatomy can be involved in the realization of different functions. For example, the hand can be used for (perceptual) exploring, but also for grasping and carrying, as well as for communicating (Gibson, 1966, p. 56). With regard to this process in the nervous system, Gibson wrote:

The same incoming nerve fiber makes a different contribution to the pickup of information from one moment to the next. [...] The individual sensory units have to function *vicariously*, to borrow a term from Lashley, a neuropsychologist. (Gibson, 1966, p. 4–5; emphasis in original)

Hence, according to Gibson, there is no one-to-one mapping between structure and function in the brain, as is commonly assumed in contemporary standard cognitive neuroscience (see Anderson, 2014 for a critical review). That is, the function of a neuron depends on the context in which it is operating. As Gibson (1966) put it, "[t]he individual nerve or neuron changes function completely when incorporated in a different system or subsystem" (p. 56). Thus, perceptual systems are constituted by both non-neural and neural anatomical structures that are temporarily assembled to establish a functional relationship with the environment—that is, to perceive a certain affordance on the basis of information. To make more explicit the fact that in the paradigmatic case anatomical structures temporarily assemble to enable the animal to *utilize* affordances (e.g., animals typically perceive to act), Reed (1982), who was inspired by both Bernstein (1967) and Gibson, introduced a *theory of action systems* as a complement to the theory of perceptual systems. As is the case with perceptual systems, the

functional animal-environment relationships that are established by action systems are typically realizable in multiple ways, that is, they are not specific to anatomical structures. For instance, the locomotor system of a human-being can manifest itself in different ways (walking, sidestepping, crawling) in which different pieces of anatomy are temporarily assembled on different occasions.

4.1. Anderson's recent theory of neural reuse

Over the past few years, Michael Anderson (Anderson, 2016, 2014, 2010, 2007; Anderson et al., 2013; Anderson and Finlay, 2014; Anderson and Penner-Wilger, 2013) has developed a view of the evolution, development and organization of the brain that is largely consistent with Gibson's tripartite theory of affordances, direct perception, and perceptual systems. Anderson is clearly inspired by Gibson's work and follows his general view on perception and action. Indeed, like Cisek (2007) and Fagg and Arbib (1998), Anderson claims that the primary function of perception is not to represent the world, but to guide an animal's actions. However, in contrast with those authors, Anderson adopts the *Gibsonian* use of the affordance concept to make this clear, placing affordances in the animal-environment relationship, rather than inside the brain.

According to the view I am describing here—following Gibson, among others—perception is primarily perception of such affordances; the world is seen as a changing set of opportunities for action and interaction, and *behavior is best explained in terms of a combination of [sic] agent's purposes and environmental structures*. (Anderson, 2014, p. 176, first emphasis in original, second emphasis added)

Moreover, although Anderson did not refer to Gibson's theory of perceptual systems, his central concept of neural reuse can be conceived of as an elaboration of the idea of *vicarious functioning* that Gibson adopted from Lashley, and that, together with *multiple realizability* (degeneracy), is central to Gibson's thinking about perceptual systems.

The concept of pluripotentiality or neural reuse refers to the idea that one and the same neural part or element is used and reused to enable multiple behavioral and cognitive functions. It is well-known that neural regions temporarily combine with other regions when animals are engaged in a task, a process referred to as functional connectivity (Bullmore and Sporns, 2009). This type of connectivity contrasts with the structural white matter fiber tracts along which these functional connections are established. The fact that functional and structural connectivity can be distinguished – with functional connectivity being highly dynamic and transient, and structural connectivity being relatively stable – arguably implies the existence of neural reuse.⁴ That is, the continual establishment of new patterns of functional connectivity indicates that neural regions connect with different other regions at different moments in time, presumably supporting a different behavioral or cognitive function in each case. Analogous to Gibson's theory of perceptual systems (1966), Anderson (2014, cf. 2010) argues that as a result of, among other sources, the different constraints imposed on a neural element when it is incorporated in one network versus another, neural elements can exist in multiple, different states, and hence may make wholly different contributions when involved in the perception or utilization of different affordances (just like the hand makes different contributions during exploring, grasping, carrying, and communicating). Anderson claims that the one-to-many structure-function mapping implied by use and reuse of neural regions in this way is the typical case. Thus, he argues that specific one-to-one structure-function mappings in the brain are

⁴ Yet, the majority of publications in contemporary cognitive neuroscience, including even the ones reporting functional connectivity data, still assume, implicitly or explicitly, a one-to-one structure-function relationship (e.g., van den Heuvel and Hulshoff Pol, 2010).

very rare, if they exist at all.

The main body of empirical evidence for this claim comes from a technique called “functional fingerprinting”. Very large amounts of neuroscientific brain activation data have been amassed since the invention of functional magnetic resonance imaging (fMRI). This technique is used to measure blood oxygenation in local brain regions while participants are engaged in a behavioral or cognitive task. The main goal of fMRI is to map the function that is indexed by the task onto a particular (set of) brain region(s). In the standard structure-function mapping approach, patterns of brain activation *within* a single task are recorded, and contrasted with patterns associated with a control task. Researchers will then conclude that the differentially activated voxels constitute the neural substrate for the task of interest (see e.g., Gallivan et al., 2013 for an example). In contrast with this approach, Anderson et al. (2013) assessed patterns of brain activation *across* a large set of controlled studies, spanning a wide range of behavioral and cognitive task domains. This allowed measurement of the number and type of tasks associated with activations in different regions of the brain. Results from this functional fingerprinting analysis showed that, regardless of the level of granularity at which the analysis was performed (i.e., whether the brain was parsed into, say, 10 or a 1000 parts), there was typically a high diversity in the kinds of tasks in which neural parts were involved. Thus, rather than functional specificity, most parts of the brain – while certainly not equipotential (cf. Lashley) – seemed to display broad functional *dispositions*. As an example, the left precentral gyrus was found to combine with different other neural regions under different task conditions. Among other regions, connections with left pars triangularis and left inferior temporal gyrus were made during ‘semantic’ tasks, but with, e.g., the brain stem and right pars triangularis during ‘emotion’ tasks, and with left precuneus and right precentral gyrus during ‘attention’ tasks (Anderson and Penner-Wilger, 2013). To stress the fact that neural parts temporarily assemble and may make different contributions depending on the neural coalitions in which they are incorporated, Anderson (2014) coins the term Transiently Assembled Local Neural Subsystems (TALoNS) “[i]n which function is temporary, repeatable, and determined by the interaction of bottom-up and top-down influences” (p. 300–301). Empirical evidence for neural reuse has been reported not just at the level of neural regions large or small but even at the level of single neurons. For example, certain neurons in *C. elegans* are capable of performing both motoric and sensory functions (White et al., 1986).

4.2. Neural parts assemble into perceptual systems and action systems to perceive and utilize affordances

Due to the methodological limitations of Gibson’s time, his assertions about multiple realizability and vicarious functioning were necessarily theoretical. As we have seen, these assertions are being borne out by recent empirical work in neuroscience (Anderson et al., 2013; Noppeney et al., 2004). As mentioned, Anderson (2014) synthesizes this work using the concepts of functional dispositions, TALoNS, and neural reuse, in which neural parts temporarily form neural coalitions with different parts at different times, and in that way are differentially involved in a range of cognitive and behavioral functions. In Gibson’s terms, anatomical structures are temporarily assembled into different perceptual and action systems, potentially playing a different role in each case. Each perceptual or action system serves to establish a different animal-environment relationship, that is, to perceive or utilize a different affordance. Anderson (2016, 2014; see also, de Wit et al., 2016; Engel et al., 2013; Kiverstein and Miller, 2015) largely follows this characterization.

We should deeply rethink the vocabulary of cognition, ideally giving the brain its voice in this process. In trying to discern what in the world the brain cares about, we should recognize that it is fundamentally an action-control system [...]. Thus, many of the properties

to which the brain is attuned are likely to be action-relevant and relational; throwability and climbability will likely be more important to the brain than weight and slope. (Anderson, 2014, p. 302)

Suggesting further that:

An organism perceives the values of salient organism–environment relationships and, in light of some goal(s), acts so as to perceive the right changes in those relationships. The brain that manages this behavior is organized in such a way that *its various parts have different dispositions to manage the values of the perceived relationships*. Interaction with an environment offering multiple affordances causes regions of the brain to be differentially activated in accordance with their functional biases. (Anderson, 2016, p. 8, emphasis added)

Crucially, the expectation of neural reuse (as well as of functional connectivity) and degeneracy follows naturally from Gibson’s theory of perceptual systems. That is, the claim that the same neural part can be temporarily assembled into different perceptual and action systems to perceive and utilize different affordances, would explicitly predict observations of neural reuse driven by the part’s disposition. Similarly, the claim that different parts can be temporarily assembled into perceptual and action systems to perceive and utilize the same affordance predicts observations of degeneracy.

Although Anderson has adopted Gibson’s concepts of information, affordances and, implicitly, perceptual systems, he is less strict in his adherence to Gibson’s rejection of the traditional subject-object framework of psychology. Indeed, Anderson (2014) argued that representations have a peripheral role in cognition (see e.g., p. 162). While this usefully contrasts with the central and foundational role that representations play in standard cognitive neuroscience, it is nevertheless problematic, because holding on to the notion of representation necessarily keeps in place the subject-object distinction and thus the divorce of the animal from its environment. In addition, Anderson (2014) also claimed that the brain engages in computation (p. 196) and that within the animal-environment relationship control localizes to the brain (see, for example, the above quotes).

However, in our view, for it to truly be a science about “us”, our ability to make our way in our worlds, and the role of the brain in this process, neuroscience needs to do away with these concepts that were copied from standard cognitive psychology.⁵ Moreover, given the Gibsonian concepts of affordances, direct perception, and perceptual systems, the concepts of computation and representation are of no explanatory value when it comes to understanding degeneracy, the continual establishment of new patterns of functional connectivity in the brain, and the neural reuse it implies. Indeed, after discarding these concepts, Anderson’s work can be used to usher Gibson’s theory of perceptual systems and Reed’s theory of action systems into contemporary neuroscience. As mentioned above, there is some empirical work on the temporary assembly of non-neural anatomical structures that occurs in the processes of perceiving and utilizing affordances (e.g., Bongers and Michaels, 2008; Carello et al., 1992; see also Bingham, 1988). The theoretical and empirical tools described by Anderson, together with the theoretical contributions of Gibson and Reed, can help neuroscientists to additionally address the role of neural parts in temporary assemblies during the perception and utilization of affordances. For example, evaluation of functional fingerprints may help to get a handle on the constraints that determine the dispositions and concomitant recruitment of neural (and non-neural) parts. Given the prevalent misuse of the affordance concept in standard cognitive neuroscience, there is currently very little relevant neuroscientific work available on the perception and utilization of affordances. An exception is arguably research on vibratory sensory substitution devices that has

⁵ At all levels, including both “higher” and “offline” cognition (see e.g., Rietveld and Brouwers, 2017; Rietveld and Kiverstein, 2014; van Dijk and Withagen, 2015, 2014).

shown that the tongue, while typically involved – as part of different action and perceptual systems – in talking or tasting, can also be deployed to detect motion of objects at a distance (and hence perceive certain affordances) resulting in activations in, among other regions, area V5 of occipital cortex of both sighted and congenitally-blind participants (Matteau et al., 2010; see also Bach-y-Rita and Kercel, 2003; Reich et al., 2012). This could point to a ‘visual’ perceptual disposition for occipital cortex, which would be consistent with its established role in vision. However, occipital cortex has also been shown to be involved in tactile discrimination tasks, even in non-blindfolded sighted participants (e.g., Zangaladze et al., 1999) which would suggest instead a more broadly defined perceptual disposition. Notably, there is evidence in congenitally-blind individuals for occipital cortex involvement during semantic language tasks (Bedny et al., 2011) implying that this particular dispositional characterization may be applicable only to sighted participants. While puzzling from a standard cognitive neuroscience perspective that presupposes one-to-one structure-function mappings, both the participation of the tongue in the perception of objects at a distance, and the involvement of occipital cortex in tactile discrimination and even language can be explained in a cogent manner from the point of view (and using the vocabulary) of Gibsonian neuroscience.

5. Concluding remarks

In this paper, we have shown how cognitive neuroscientists increasingly make use of Gibson’s concept of affordance when discussing the role of the brain in perception and action. Under the influence of Jeannerod (e.g., 1994), the concept has typically been used to refer to (action-oriented) representations *in the brain*, reinstating the distinction between subject and object that has held psychology captive since the 17th century. We explained in detail how this use of the concept is neither in line with Gibson’s intention to overcome the subject-object framework, nor with his thinking about the role of the brain in the perception of affordances. According to Gibson, neural regions are parts of perceptual systems, temporary assemblies of anatomical structures with which animals establish functional relationships with the environment—that is, with which they perceive affordances on the basis of information. Anatomical structures can make different contributions to function depending on the perceptual system in which they are incorporated, and the recruitment of a particular anatomical structure is limited in principle only by its structural and morphological constraints. Anderson (2014) has developed a theory of the brain using the concepts of neural reuse, TALoNS and functional dispositions that can be seen as an elaboration of Gibson’s theory of perceptual systems. When appropriately analyzed, the body of available fMRI data is in line with this theory. Relying on Anderson (2014), minus some remaining debris from standard cognitive psychology, we described the outlines of a Gibsonian neuroscience aimed at understanding how embodied animals embedded or situated in environments regulate their encounters with the affordances of their environments. The next steps should be to develop feasible neuroscientific paradigms with which to test for the presence of neural reuse and degeneracy during affordance perception and utilization – properly construed – and in this way further sharpen and deepen the ecological study of the brain.

References

Adolph, K.E., Eppler, M.A., Gibson, E.J., 1993. Crawling versus walking infants’ perception of affordances for locomotion over sloping surfaces. *Child Dev.* 64, 1158–1174. <http://dx.doi.org/10.1111/j.1467-8624.1993.tb04193.x>.

Anderson, M.L., Finlay, B.L., 2014. Allocating structure to function: the strong links between neuroplasticity and natural selection. *Front. Hum. Neurosci.* 7, 918. <http://dx.doi.org/10.3389/fnhum.2013.00918>.

Anderson, M.L., Penner-Wilger, M., 2013. Neural reuse in the evolution and development of the brain: evidence for developmental homology? *Dev. Psychobiol.* 55, 42–51. <http://dx.doi.org/10.1002/dev.21055>.

Anderson, M.L., Kinnison, J., Pessoa, L., 2013. Describing functional diversity of brain

regions and brain networks. *Neuroimage* 73, 50–58. <http://dx.doi.org/10.1016/j.neuroimage.2013.01.071>.

Anderson, M.L., 2007. Evolution of cognitive function via redeployment of brain areas. *Neuroscience* 13, 13–21. <http://dx.doi.org/10.1177/1073858406294706>.

Anderson, M.L., 2010. Neural reuse: a fundamental organizational principle of the brain. *Behav. Brain Sci.* 33, 245–266. <http://dx.doi.org/10.1017/S0140525X10000853>.

Anderson, M.L., 2014. *After Phrenology: Neural Reuse and the Interactive Brain*. The MIT Press, Cambridge, MA.

Anderson, M.L., 2016. Précis of after phrenology: neural reuse and the interactive brain. *Behav. Brain Sci.* 39, e120. <http://dx.doi.org/10.1017/S0140525X15000631>.

Bach, P., Nicholson, T., Hudson, M., 2014. The affordance-matching hypothesis: how objects guide action understanding and prediction. *Front. Hum. Neurosci.* 8, 254. <http://dx.doi.org/10.3389/fnhum.2014.00254>.

Bach-y-Rita, P., Kercel, S.W., 2003. Sensory substitution and the human-machine interface. *Trends Cogn. Sci.* 7, 541–546. <http://dx.doi.org/10.1016/j.tics.2003.10.013>.

Bedny, M., Pascual-Leone, A., Dodell-Feder, D., Fedorenko, E., Saxe, R., 2011. Language processing in the occipital cortex of congenitally blind adults. *Proc. Natl. Acad. Sci. U. S. A.* 108, 4429–4434. <http://dx.doi.org/10.1073/pnas.1014818108>.

Bernstein, N.A., 1967. *The Coordination and Regulation of Movements*. Pergamon Press, Oxford.

Bingham, G.P., 1988. Task-specific devices and the perceptual bottleneck. *Hum. Mov. Sci.* 7, 225–264. [http://dx.doi.org/10.1016/0167-9457\(88\)90013-9](http://dx.doi.org/10.1016/0167-9457(88)90013-9).

Bongers, R.M., Michaels, C.F., 2008. The role of eye and head movements in detecting information about fly balls. *J. Exp. Psychol. Hum. Percept. Perform.* 34, 1515–1523. <http://dx.doi.org/10.1037/a0011974>.

Bruineberg, J., Rietveld, E., 2014. Self-organization, free energy minimization, and optimal grip on a field of affordances. *Front. Hum. Neurosci.* 8, 599. <http://dx.doi.org/10.3389/fnhum.2014.00599>.

Buccino, G., Sato, M., Cattaneo, L., Rodà, F., Riggio, L., 2009. Broken affordances, broken objects: a TMS study. *Neuropsychologia* 47, 3074–3078. <http://dx.doi.org/10.1016/j.neuropsychologia.2009.07.003>.

Bullmore, E., Sporns, O., 2009. Complex brain networks: graph theoretical analysis of structural and functional systems. *Nat. Rev. Neurosci.* 10, 186–198. <http://dx.doi.org/10.1038/nrn2575>.

Carello, C., Fitzpatrick, P., Domaniewicz, I., Chan, T.-C., Turvey, M.T., 1992. Effortful touch with minimal movement. *J. Exp. Psychol. Hum. Percept. Perform.* 18, 290–302. <http://dx.doi.org/10.1037/0096-1523.18.1.290>.

Chapman, S., 1968. Catching a baseball. *Am. J. Phys.* 36, 868. <http://dx.doi.org/10.1119/1.1974297>.

Chemero, A., 2003. An outline of a theory of affordances. *Ecol. Psychol.* 15, 181–195. http://dx.doi.org/10.1207/S15326969ECO1502_5.

Cisek, P., Kalaska, J.F., 2010. Neural mechanisms for interacting with a world full of action choices. *Annu. Rev. Neurosci.* 33, 269–298. <http://dx.doi.org/10.1146/annurev.neuro.051508.135409>.

Cisek, P., Pastor-Bernier, A., 2014. On the challenges and mechanisms of embodied decisions. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 369, 20130479. <http://dx.doi.org/10.1098/rstb.2013.0479>.

Cisek, P., 2007. Cortical mechanisms of action selection: the affordance competition hypothesis. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 362, 1585–1599. <http://dx.doi.org/10.1098/rstb.2007.2054>.

Costall, A., Morris, P., 2015. The textbook Gibson: the assimilation of dissidence. *Hist. Psychol.* 18, 1–14. <http://dx.doi.org/10.1037/a0038398>.

Costall, A., 1995. Socializing affordances. *Theory Psychol.* 5, 467–481. <http://dx.doi.org/10.1177/0959354395054001>.

Costall, A., 1999. An iconoclast’s triptych: Edward Reed’s ecological philosophy. *Theory Psychol.* 9, 411–416. <http://dx.doi.org/10.1177/0959354399093011>.

Costall, A., 2004. From Darwin to Watson (and cognitivism) and back again: the principle of animal-environment mutuality. *Behav. Philos.* 32, 179–195.

Creem-Regehr, S.H., Lee, J.N., 2005. Neural representations of graspable objects: are tools special? *Cogn. Brain Res.* 22, 457–469. <http://dx.doi.org/10.1016/j.cogbrainres.2004.10.006>.

Declerck, G., 2013. Why motor simulation cannot explain affordance perception. *Adapt. Behav.* 21, 286–298. <http://dx.doi.org/10.1177/1059712313488424>.

Dennett, D.C., 1998. *Brainchildren: Essays On Designing Minds*. The MIT Press, Cambridge MA.

de Vries, S., Withagen, R., Zaal, F.T.J.M., 2015. Transfer of attunement in length perception by dynamic touch. *Atten. Percept. Psychophys.* 77, 1396–1410. <http://dx.doi.org/10.3758/s13414-015-0872-y>.

de Wit, M.M., van der Kamp, J., Withagen, R., 2016. Gibsonian neuroscience. *Theory Psychol.* 26, 413–415. <http://dx.doi.org/10.1177/0959354315623109>.

Dijksterhuis, E.J., 1950. *De mechanisering van het wereldbeeld*. Meulenhoff, Amsterdam.

Dotov, D.G., Nie, L., Wit de, M.M., 2012. Understanding affordances: history and contemporary development of Gibson’s central concept. *Avant* 3, 28–39.

Ellis, R., Tucker, M., 2000. Micro-affordance: the potentiation of components of action by seen objects. *Br. J. Psychol.* 91, 451–471. <http://dx.doi.org/10.1348/000712600161934>.

Engel, A.K., Maye, A., Kurthen, M., König, P., 2013. Where’s the action? The pragmatic turn in cognitive science. *Trends Cogn. Sci.* 17, 202–209. <http://dx.doi.org/10.1016/j.tics.2013.03.006>.

Evans, C., Edwards, M.G., Taylor, L.J., Ietswaart, M., 2016. Impaired communication between the dorsal and ventral stream: indications from apraxia. *Front. Hum. Neurosci.* 10, 8. <http://dx.doi.org/10.3389/fnhum.2016.00008>.

Fagg, A.H., Arbib, M.A., 1998. Modeling parietal-premotor interactions in primate control of grasping. *Neural Netw.* 11, 1277–1303. [http://dx.doi.org/10.1016/S0893-6080\(98\)00047-1](http://dx.doi.org/10.1016/S0893-6080(98)00047-1).

Fajen, B.R., 2005a. Calibration, information, and control strategies for braking to avoid a

- collision. *J. Exp. Psychol. Hum. Percept. Perform.* 31, 480–501. <http://dx.doi.org/10.1037/0096-1523.31.3.480>.
- Fajen, B.R., 2005b. The scaling of information to action in visually guided braking. *J. Exp. Psychol. Hum. Percept. Perform.* 31, 1107–1123. <http://dx.doi.org/10.1167/4.8.811>.
- Franchak, J.M., van der Zalm, D.J., Adolph, K.E., 2010. Learning by doing: action performance facilitates affordance perception. *Vis. Res.* 50, 2758–2765. <http://dx.doi.org/10.1016/j.visres.2010.09.019>.
- Fuster, J.M., 2000. The module: crisis of a paradigm. *Neuron* 26, 51–53. [http://dx.doi.org/10.1016/S0896-6273\(00\)81137-X](http://dx.doi.org/10.1016/S0896-6273(00)81137-X).
- Gallivan, J.P., McLean, D.A., Valyear, K.F., Culham, J.C., 2013. Decoding the neural mechanisms of human tool use. *Elife* 2, e00425. <http://dx.doi.org/10.7554/eLife.00425>.
- Gibson, J.J., 1958. Visually controlled locomotion and visual orientation in animals. *Br. J. Psychol.* 49, 182–194. <http://dx.doi.org/10.1111/j.2044-8295.1958.tb00656.x>.
- Gibson, J.J., 1966. *The Senses Considered As Perceptual Systems*. Houghton Mifflin, Boston, MA.
- Gibson, J.J., 1986. *The Ecological Approach to Visual Perception*. Houghton Mifflin, Boston, MA. Original work published 1979.
- Grèzes, J., Decety, J., 2002. Does visual perception of object afford action? Evidence from a neuroimaging study. *Neuropsychologia* 40, 212–222. [http://dx.doi.org/10.1016/S0028-3932\(01\)00089-6](http://dx.doi.org/10.1016/S0028-3932(01)00089-6).
- Jeannerod, M., Arbib, M.A., Rizzolatti, G., Sakata, H., 1995. Grasping objects: the cortical mechanisms of visuomotor transformation. *Trends Neurosci.* 18, 314–320. [http://dx.doi.org/10.1016/0166-2236\(95\)93921-J](http://dx.doi.org/10.1016/0166-2236(95)93921-J).
- Jeannerod, M., 1994. The representing brain: neural correlates of motor intention and imagery. *Behav. Brain Sci.* 17, 187. <http://dx.doi.org/10.1017/S0140525X00034026>.
- Jeannerod, M., 2001. Neural simulation of action: a unifying mechanism for motor cognition. *Neuroimage* 14, S103–S109. <http://dx.doi.org/10.1006/nimg.2001.0832>.
- Kühn, S., Werner, A., Lindenberger, U., Verrel, J., 2014. Acute immobilisation facilitates premotor preparatory activity for the non-restrained hand when facing grasp affordances. *Neuroimage* 92, 69–73. <http://dx.doi.org/10.1016/j.neuroimage.2014.02.003>.
- Kanwisher, N., 2010. Functional specificity in the human brain: a window into the functional architecture of the mind. *Proc. Natl. Acad. Sci. U. S. A.* 107, 11163–11170. <http://dx.doi.org/10.1073/pnas.1005062107>.
- Kiverstein, J., Miller, M., 2015. The embodied brain: towards a radical embodied cognitive neuroscience. *Front. Hum. Neurosci.* 9, 1–11. <http://dx.doi.org/10.3389/fnhum.2015.00237>.
- Kugler, P., Turvey, M.T., 1987. *Information, Natural Law, and The Self-Assembly of Rhythmic Movement*. Lawrence Erlbaum Associates, Hillsdale.
- Makris, S., Hadar, A.A., Yarrow, K., 2013. Are object affordances fully automatic? A case of covert attention. *Behav. Neurosci.* 127, 797–802. <http://dx.doi.org/10.1037/a0033946>.
- Mark, L.S., 1987. Eyeheight-scaled information about affordances: a study of sitting and stair climbing. *J. Exp. Psychol. Hum. Percept. Perform.* 13, 361–370. <http://dx.doi.org/10.1037/0096-1523.13.3.361>.
- Martensen, R.L., 2004. *The Brain Takes Shape: An Early History*. Oxford University Press, Oxford.
- Matteau, I., Kupers, R., Ricciardi, E., Pietrini, P., Ptitto, M., 2010. Beyond visual, aural and haptic movement perception: hMT+ is activated by electrostatic motion stimulation of the tongue in sighted and in congenitally blind individuals. *Brain Res. Bull.* 82, 264–270. <http://dx.doi.org/10.1016/j.brainresbull.2010.05.001>.
- Michaels, C.F., Zeinstra, E.B., Oudejans, R.R., 2001. Information and action in punching a falling ball. *Q. J. Exp. Psychol. A* 54, 69–93. <http://dx.doi.org/10.1080/02724980042000039>.
- Mon-Williams, M., Bingham, G.P., 2011. Discovering affordances that determine the spatial structure of reach-to-grasp movements. *Exp. Brain Res.* 211, 145–160. <http://dx.doi.org/10.1007/s00221-011-2659-2>.
- Noppeney, U., Friston, K.J., Price, C.J., 2004. Degenerate neuronal systems sustaining cognitive functions. *J. Anat.* 205, 433–442. <http://dx.doi.org/10.1111/j.0021-8782.2004.00343.x>.
- Oudejans, R.R.D., Michaels, C.F., Bakker, F.C., Dolné, M.A., 1996. The relevance of action in perceiving affordances: perception of catchableness of fly balls. *J. Exp. Psychol. Hum. Percept. Perform.* 22, 879–891. <http://dx.doi.org/10.1037/0096-1523.22.4.879>.
- Pagano, C.C., Fitzpatrick, P.M., Turvey, M.T., 1993. Tensorial basis to the constancy of perceived object extent over variations of dynamic touch. *Percept. Psychophys.* 54, 43–54. <http://dx.doi.org/10.3758/BF03206936>.
- Pezzulo, G., Cisek, P., 2016. Navigating the affordance landscape: feedback control as a process model of behavior and cognition. *Trends Cogn. Sci.* 20, 414–424. <http://dx.doi.org/10.1016/j.tics.2016.03.013>.
- Price, C.J., Friston, K.J., 2002. Degeneracy and cognitive anatomy. *Trends Cogn. Sci.* 6, 416–421. [http://dx.doi.org/10.1016/S1364-6613\(02\)01976-9](http://dx.doi.org/10.1016/S1364-6613(02)01976-9).
- Proctor, R.W., Miles, J.D., 2014. Does the concept of affordance add anything to explanations of stimulus-response compatibility effects? *Psychology of Learning and Motivation – Advances in Research and Theory*, 1st ed. Elsevier Inc. <http://dx.doi.org/10.1016/B978-0-12-800090-8.00006-8>.
- Proverbio, A.M., Azzari, R., Adorni, R., 2013. Is there a left hemispheric asymmetry for tool affordance processing? *Neuropsychologia* 51, 2690–2701. <http://dx.doi.org/10.1016/j.neuropsychologia.2013.09.023>.
- Reed, E., 1982. An outline of a theory of action systems. *J. Motor Behav.* 14, 98–134. <http://dx.doi.org/10.1080/00222895.1982.10735267>.
- Reed, E.S., 1996. *Encountering the World: Toward an Ecological Psychology*. Oxford University Press, New York. <http://dx.doi.org/10.1093/acprof:oso/9780195073010.001.0001>.
- Reich, L., Maidenbaum, S., Amedi, A., 2012. The brain as a flexible task machine. *Curr. Opin. Neurol.* 25, 86–95. <http://dx.doi.org/10.1097/WCO.0b013e32834ed723>.
- Rietveld, E., Brouwers, A.A., 2017. Optimal grip on affordances in architectural design practices: an ethnography. *Phenomenol. Cogn. Sci.* 16, 545–564. <http://dx.doi.org/10.1007/s11097-016-9475-x>.
- Rietveld, E., Kiverstein, J., 2014. A rich landscape of affordances. *Ecol. Psychol.* 26, 325–352. <http://dx.doi.org/10.1080/10407413.2014.958035>.
- Sakreida, K., Effner, L., Thill, S., Menz, M.M., Jirak, D., Eickhoff, C.R., Ziemke, T., Eickhoff, S.B., Borghi, A.M., Binkofski, F., 2016. Affordance processing in segregated parieto-frontal dorsal stream sub-pathways. *Neurosci. Biobehav. Rev.* 69, 89–112. <http://dx.doi.org/10.1016/j.neubiorev.2016.07.032>.
- Solomon, H.Y., Turvey, M.T., 1988. Haptically perceiving the distances reachable with hand-held objects. *J. Exp. Psychol. Hum. Percept. Perform.* 14, 404–427. <http://dx.doi.org/10.1037/0096-1523.14.3.404>.
- Sporns, O., 2011. *Networks of the Brain*. The MIT Press, Cambridge, MA.
- Symes, E., Ellis, R., Tucker, M., 2007. Visual object affordances: object orientation. *Acta Psychol. (Amst.)* 124, 238–255. <http://dx.doi.org/10.1016/j.actpsy.2006.03.005>.
- Tresilian, J.R., 1999. Visually timed action: time-out for tau? *Trends Cogn. Sci.* 3, 301–310. [http://dx.doi.org/10.1016/S1364-6613\(99\)01352-2](http://dx.doi.org/10.1016/S1364-6613(99)01352-2).
- Tucker, M., Ellis, R., 1998. On the relations between seen objects and components of potential actions. *J. Exp. Psychol. Hum. Percept. Perform.* 24, 830–846. <http://dx.doi.org/10.1037/0096-1523.24.3.830>.
- Tucker, M., Ellis, R., 2001. The potentiation of grasp types during visual object categorization. *Vis. Cogn.* 8, 769–800. <http://dx.doi.org/10.1080/13506280042000144>.
- Tucker, M., Ellis, R., 2004. Action priming by briefly presented objects. *Acta Psychol. (Amst.)* 116, 185–203. <http://dx.doi.org/10.1016/j.actpsy.2004.01.004>.
- Turvey, M.T., 1992. Affordances and prospective control: an outline of the ontology. *Ecol. Psychol.* 4, 173–187. http://dx.doi.org/10.1207/s15326969eco0403_3.
- Valyear, K.F., Gallivan, J.P., McLean, D.A., Culham, J.C., 2012. fMRI repetition suppression for familiar but not arbitrary actions with tools. *J. Neurosci.* 32, 4247–4259. <http://dx.doi.org/10.1523/JNEUROSCI.5270-11.2012>.
- van Dijk, L., Withagen, R., 2014. The horizontal worldview: a Wittgensteinian attitude towards scientific psychology. *Theory Psychol.* 24, 3–18. <http://dx.doi.org/10.1177/0959354313517415>.
- van Dijk, L., Withagen, R., 2015. Temporalizing agency: moving beyond on- and offline cognition. *Theory Psychol.* 26, 5–26. <http://dx.doi.org/10.1177/0959354315596080>.
- van Hof, P., van der Kamp, J., Savelsbergh, G.J.P., 2008. The relation between infants' perception of catchableness and the control of catching. *Dev. Psychol.* 44, 182–194. <http://dx.doi.org/10.1037/0012-1649.44.1.182>.
- van den Heuvel, M.P., Hulshoff Pol, H.E., 2010. Exploring the brain network: a review on resting-state fMRI functional connectivity. *Eur. Neuropsychopharmacol.* 20, 519–534. <http://dx.doi.org/10.1016/j.euroneuro.2010.03.008>.
- van der Meer, A.L.H., Svantesson, M., van der Weel, F.R.R., 2013. Longitudinal study of looming in infants with high-density EEG. *Dev. Neurosci.* 34, 488–501. <http://dx.doi.org/10.1159/000345154>.
- Walls, G.L., 1942. *The Vertebrate Eye and Its Adaptive Radiation*. Cranbrook Institute of Science, Bloomfield Hills, MI.
- Warren, W.H., Kay, B., Zosh, W., Duchon, A., Sahuc, S., 2001. Optic flow is used to control human walking. *Nat. Neurosci.* 4, 213–216. <http://dx.doi.org/10.1038/84054>.
- Warren, W.H., 1984. Perceiving affordances: visual guidance of stair climbing. *J. Exp. Psychol. Hum. Percept. Perform.* 10, 683–703. <http://dx.doi.org/10.1037/0096-1523.10.5.683>.
- White, J.G., Southgate, E., Thomson, J.N., Brenner, S., 1986. The structure of the nervous system of the nematode *Caenorhabditis elegans*. *Philos. Trans. R. Soc. B* 314, 1–340.
- Withagen, R., Michaels, C.F., 2004. Transfer of calibration in length perception by dynamic touch. *Percept. Psychophys.* 66, 1282–1292. <http://dx.doi.org/10.3758/BF03194998>.
- Withagen, R., Michaels, C.F., 2005. On ecological conceptualizations of perceptual systems and action systems. *Theory Psychol.* 15, 603–620. <http://dx.doi.org/10.1177/0959354305057265>.
- Zangaladze, A., Epstein, C.M., Grafton, S.T., Sathian, K., 1999. Involvement of visual cortex in tactile discrimination of orientation. *Nature* 401, 587–590. <http://dx.doi.org/10.1038/44139>.
- Zhu, Q., Bingham, G.P., 2011. Human readiness to throw: the size-weight illusion is not an illusion when picking the best objects to throw. *Evol. Hum. Behav.* 32, 288–293. <http://dx.doi.org/10.1016/j.evolhumbehav.2010.11.005>.
- Zimmer, C., 2004. *Soul Made Flesh: The Discovery of the Brain and How It Changed the World*. Free Press, New York.