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The Brain Evolved to Guide Action

Michael Anderson and Anthony Chemero

1.1 Introduction

In the 19th century, major movements in both psychology and neuroscience were profoundly influenced by Darwin. William James argued for a view of psychology which ultimately came to be known as functionalism; in neuroscience, Herbert Spencer and Santiago Ramon y Cajal argued that we needed to study the mind and brain as adaptations to the environment. In both cases, this evolutionary approach forced a focus on the role of the brain in action guidance. These approaches were revived at the end of the 20th century in the form of embodied cognitive science, which focuses on the importance of action in understanding cognition. Embodied cognitive science calls for an understanding of the brain as having evolved initially for perception and action. It suggests that even complex cognitive abilities such as language and reasoning will use neural resources which initially evolved to guide action. We close by providing evidence that this is, in fact, how the human brain evolved.

1.2 William James and the Functionalist Tradition

In the *Principles of Psychology* (1890), William James described a plan of research for psychology that put front and center both the brain and evolution by natural selection. In the introductory chapter, James contrasted his approach with that of prior (nonscientific) psychologists by pointing out the necessity of the brain for the existence of any experience at all.

The fact that the brain is the one immediate bodily condition of the mental operations is indeed so universally admitted nowadays that I need spend no more time in illustrating it, but will simply postulate it and pass on. The whole remainder of the book will be more or less of a proof that the postulate was correct. (James, 1890, p. 4)

Modern psychologists of the late 19th century, James wrote, had to be “cerebralists” (p. 5). At the same time, however, James felt that psychology could not be *only* about the brain.

it will be safe to lay down the general law that *no mental modification ever occurs which is not accompanied or followed by a bodily change*. The ideas and feelings, e.g., which these present printed characters excite in the reader’s mind not only occasion movements of his eyes and nascent movements of articulation in him, but will some day make him speak, or take sides in a discussion, or give advice, or choose a book to read, differently from what would have been the case had they never impressed his retina. Our psychology must therefore take account not only of the conditions antecedent to mental states, but of their resultant consequences as well. (James, 1890, p. 5)

Focusing on the brain as the “immediate bodily condition” of the mind, then, required that we understand the brain in light of its (eventual) connections to actions that we engage in.

This last point is a consequence of Darwin’s influence on James. Following Herbert Spencer (1855), James thought the purpose of the mind is to adapt to us to the environment. As Spencer put it:

The fundamental condition of vitality, is, that the internal order shall be continually adjusted to the external order. If the internal order is altogether unrelated to the external order, there can be no adaptation between the actions going on in the organism and those going on in its environment: and life becomes impossible. (Spencer, 1855: §173)

Such adaptation occurs only via action that adjusts the body so that it fits in with the world. Thus, for James, the subject matter of psychology had to be *every* aspect of our mental life, understood in the context of how it adapts us to the environment. It is this feature of Jamesian psychology that led him and his followers to be condescendingly called *functionalists* (Titchener, 1898), because they believed that the way to do psychology was to understand thoughts, habits, emotions, etc. in terms of their adaptive function. Because James was a cerebralist, the same has to be true of the parts of the brain that are these thoughts’, habits’, and emotions’ “immediate bodily conditions”. Indeed, Chapter 2 of the *Principles* is called “The Functions of the Brain.”

James’s combination of functionalism and cerebralism, then, committed him to specific views concerning the evolution of the brain. To understand consciousness, for example, would be to understand how consciousness adapts an animal to its environment. But this adaptation to the environment can only be understood in terms of the other aspects of the animal’s life right now, over developmental time, and over phylogenetic time.

It is very generally admitted, though the point would be hard to prove, that consciousness grows the more complex and intense the higher we rise in the animal kingdom. That of a man must exceed that of an oyster. From this point of view it seems an organ, superadded to the other organs which maintain the animal in the struggle for existence; and the presumption of course is that it helps him in some way

in the struggle, just as they do. But it cannot help him without being in some way efficacious and influencing the course of his bodily history. (James 1890, p. 138)

Brains evolved to guide adaptive action, and human-specific actions must result from evolutionary “superaddition” on to the abilities of human ancestors.

Jamesian functionalism and cerebralism were the dominant views in American psychology for roughly the first half of the 20th century, up until the cognitive revolution. The counterpart view in the neurosciences was not so long-lived.

1.3 Ramon y Cajal’s Functionalist Neuroscience

Like James, Spanish neuroanatomist Santiago Ramon y Cajal was influenced by Spencer’s evolutionary approach to understanding brain and behavior. Spencer argued that one had to approach the investigation of life and mind taking fundamental principles into account: First was the primacy of adaptation, the continual adjustment of inner to outer conditions. Second was a principle of growth and development, whereby both an organism’s repertoire of responses and the biological structures supporting them increase in number, diversity, and complexity. Organisms evolve and develop by becoming at one and the same time more differentiated and more integrated or coordinated in both structure and behavior. It is from these parallel developments (and not from either acting alone) that the increasing complexity of organisms emerges over time.

In the progress from an eye that appreciates only the difference between light and darkness, to one which appreciates degrees of difference between them, and afterwards to one which appreciates differences of colour and degrees of colour—in the progress from the power of distinguishing a few strongly contrasted smells or tastes, to the power of distinguishing an infinite variety of slightly contrasted smells or tastes ... in all those cases which present merely a greater ability to discriminate between varieties of the same simple phenomenon; there is increase in the speciality of the correspondence without increase in its complexity... But where the stimulus responded to, consists, not of a single sensation but of several; or where the response is not one action but a group of actions; the increase in speciality of correspondence results from an increase in its complexity. (Spencer 1855: §154)

Finally, there was the principle of continuity, which stated that new developments emerge from, build upon, and (partly) preserve what came before. This implied not just that organisms can be arrayed on a biological and psychological continuum, with many differences in degree but few fundamental discontinuities between the mental powers of “higher” and “lower” organisms, but also that, within each organism, the higher mental faculties develop from and rest upon the foundations of the lower. As Robert Wozniak commented:

The implications of these evolutionary conceptions ... are clear. The brain is the most highly developed physical system we know and the cortex is the most developed level of the brain. As such, it must be heterogeneous, differentiated, and complex. Furthermore, if the cortex is a continuous development from sub-cortical structures,

the sensory-motor principles that govern sub-cortical localization must hold in the cortex as well. Finally, if higher mental processes are the end product of a continuous process of development from the simplest irritation through reflexes and instincts, there is no justification for drawing a sharp distinction between mind and body. The mind/body dichotomy that for two centuries had supported the notion that the cerebrum, functioning as the seat of higher mental processes, must function according to principles radically different from those descriptive of sub-cerebral nervous function, had to be abandoned. (Wozniak, 1992)

Ramon y Cajal took Spencer's principles to heart, and clearly saw them reflected in the neural structures that he was so adept at describing. It is perhaps easiest to start with his summary of three trends in the evolution of neural organization that he observed. The first was a "proliferation of neurons and neuronal processes that ... increased the complexity of relationships between various tissues and organs" (Ramon y Cajal, 1904/1995, p. 11). Such proliferation was necessitated by the increase in the number and complexity of *other* cells in the organism that is observed over evolutionary time. As Ramon y Cajal pointed out, an increase in the size and complexity of an organism without an attendant increase in the number of neural cells it possesses would precipitate a decrease in sensory acuity and presumably in agility as well, given the increase in the ratio between body parts and the sensory and motor neurons that would serve them. Ramon y Cajal tied neural development especially closely to the motor system:

Once it has appeared, the nervous system comes to direct the muscular system through a series of actions and reactions. Indeed, because of the concurrent specializations that occur in animals, both the nervous system and the muscular system not only appear together, but are also functionally interdependent. (Ramon y Cajal 1904/1995, p. 5)

The second evolutionary trend detailed by Ramon y Cajal was "an adaptive differentiation of neuronal morphology and fine structure." The third was "a progressive unification of the nervous system, a concentration of its elements into neural masses" (Ramon y Cajal 1904/1995, p. 12)—that is, the emergence of central ganglia including the brain and spinal cord. The effect of this centralization is crucial to function:

Motor neurons that before were peripheral and isolated from one another are now juxtaposed in a single, central nucleus; they are transversely integrated, to use Herbert Spencer's phrase. ... the sensory neurons can excite all of the aggregated motor neurons, and only a few additional expansions are necessary for the sensory arborizations to expand their spheres of motor influence (Ramon y Cajal 1904/1995, p. 14)

In what must appear a paradox to those accustomed to understanding the brain in terms of the localization of psychological faculties, the anatomic consolidation that Ramon y Cajal described permits function to be *less* localized, even as the supporting tissues become more central. This arrangement makes perfect sense when one expects the brain to be, rather than a collection of organs with distinct local functions, a

structure establishing functional *relationships* between cells to coordinate the organism's interaction with its environment.

Ramon y Cajal argued that coordination, control, and complexity are achieved via the emergence of two new classes of neural cells in addition to sensory and motor neurons: association neurons and psychomotor neurons. Association neurons mediate the link between sensory and motor cells, allowing the emergence of complex responses to sensory stimuli.

With the association neuron, multicellular organisms become true animals. Sensory stimuli, even if localized to one point on the integument, are no longer isolated ... The association pathways that interrelate various muscle fields and the areas of the integument with which they are connected are by no means randomly distributed. Evolution and adaptation have determined their organization, and the precision of their distribution is such that each stimulus received by a sensory cell causes the animal to respond with what Exner has called a *combination of movements*, that is to say, with a complex movement that is appropriately coordinated for the animal's self-preservation and procurement of nutritional requirements. (Ramon y Cajal 1904/1995, pp. 5, 7)

Psychomotor neurons were understood by Ramon y Cajal to be exceptionally powerful and centralized association neurons, able to exert their influence over an extraordinarily broad range of circumstances and behaviors. Psychomotor neurons are able to modulate behavior based not just on external stimuli, but also on internal conditions, and not just on current stimulation but also past experience.

In the evolution of the nervous system, this element, which underlies the still largely unexplored world of psychological (psychic) phenomena, is a more recent addition than the association neuron. It too is interpolated between sensory and motor neurons, but at a distance, and is generally located in one particular ganglion: the cerebral ganglion of invertebrates and the cerebral cortex of vertebrates.... The empire of the psychomotor neuron, together with the various ganglia distributed throughout the body, constitute the organism's newest and most useful weapons in the struggle for survival. (Ramon y Cajal 1904/1995, p. 8)

Ramon y Cajal's choice of metaphor is striking, for, in his view, the psychomotor neuron truly does rule over vast swaths of behavior. Two things especially are important to note: the first is that the regulatory capacity of the psychomotor neuron is made possible only because the centralization of neural structures permits single cells to quickly and specifically affect a wide range of inputs and outputs; the second is that the power of psychomotor neurons does not lie in their *intrinsic* properties but rather in their defining functional *relationships*.

Wherein lies the superiority—the supremacy—of the cephalic ganglion? In our view it derives from the inherent superiority of the functional relationships established between the external world and this ganglion. Let us explain. The abdominal ganglia are linked to the sensory nerve cells that relay simple, rather poorly defined and crude tactile and thermal sensations from the integument. The cephalic ganglion, in

contrast, is connected to the very specialized neurons that subserve vision, hearing and smell, and this receives preorganized patterns (including more complex temporal and spatial information) that provide the most accurate representations of the external world. This difference in type of connections is mostly responsible for the preeminence of the cerebral ganglion. And the eye and the ear are the major artisans of this preeminence. In essence these organs are *computational devices*, to use Max Nordau's pleasing expression, that select in a very specific way from the middle range of the immensely broad energy spectrum those wavelengths for which they are adapted. (Ramon y Cajal 1904/1995, p. 8)

Interestingly, for Ramon y Cajal the precision and accuracy with which the sense organs represent the external world obviates the need for central structures to do so.

The cerebral cortex of vertebrates, and the cerebral ganglion of invertebrates, do not need to create images; complete images are formed by the sense organs and supplied instead to the cerebral cortex or cerebral ganglion in highly refined ways that actually reflect the intensity and all the subtle nuances inherent in the excitatory stimuli. In the final analysis, the marvelous structural organization of the eye and ear is the primary reason for the dominant position of the cerebral cortex. (Ramon y Cajal 1904/1995, pp. 8–9)

There is much that is striking in Ramon y Cajal's perspective. First is his focus not on intrinsic function or localized faculties in the regions of the brain but rather on the establishment of functional relationships. Indeed, Ramon y Cajal took this perspective so seriously that he was led to predict the outcome of experiments—different in detail but identical in intent—first performed over 80 years after the time of his writing (e.g., Sur, Garraghty, & Roe, 1988):

Insights provided by the evolution of central neural centers have now so convinced us of the preeminent role played by the nature of their relationship to the external world that we are tempted to propose the following: If by some capricious and seemingly impossible developmental anomaly the optic nerve should end in the spinal cord, visual sensations would be elaborated in the region occupied by motor neurons! (Ramon y Cajal 1904/1995, p. 9)

It is worth emphasizing an important consequence of this focus on neural relationships: Differences in neural morphology should not be taken to indicate differences in intrinsic function but rather to indicate different abilities to establish sorts of functional connections or coordination. It is only for this reason that anatomic, morphological differentiation can effect increasing functional—which is to say behavioral—complexity.

Second, we see a recognition here of the importance of peripheral structures to cognition, not just as input channels but as organs of cognition in their own right. Indeed, it would not be inappropriate to see, in Ramon y Cajal's insight that sense organs play a role in selecting and structuring stimuli, a precursor to current recognition of the importance of bodily activity and morphology in cognitive processes (Anderson, 2003; Barrett, 2011; Chemero, 2009), including such recently emerging notions as morphological computation (Paul, Lungarella, & Iida 2006). Cephalopods,

for instance, take advantage of various limb properties to make the inverse kinematics problem they must solve to compute limb movements much simpler than it would otherwise be in their extremely flexible extremities (Hochner, 2012).

Third, and finally, there is the fundamental orientation toward action:

What utilitarian goal has nature (which never seems to act in vain) pursued in forcing nervous system differentiation to these lengths? ... [T]he refinement and enhancement of reflex activity, which protects the life of both the individual and the species. ... Such reflexes constitute the fundamental repository of neural adaptations that provide an animal with the necessities of life ... To the hierarchy of increasingly more complex reflexes—irritability in protozoa, simple reflexes in lower vertebrates, and more complex reflexes in higher invertebrates and vertebrates—one must add the all-powerful psychic reflex of vertebrates, and especially the higher vertebrates. In the latter ... neural and nonneural structures are not simply under the influence of external stimuli; they are also subject to internal stimuli arising from control centers within the organism itself. (Ramon y Cajal 1904/1995, p. 16)

For Ramon y Cajal, the *telos* of cognition is action, and for this reason even “complex and deferred responses ... are true reflexes” (Ramon y Cajal 1904/1995, p. 17). Since in our time we tend to reserve the term “reflex” for those simple, stereotyped (and generally spinally mediated) motor responses to strong, simple stimuli, it would be easy to dismiss Ramon y Cajal’s view here as not reflecting the true complexity of the brain’s function. In point of fact, given his insistence on a “hierarchy” of reflexes, and the more general point that evolution tends to preserve, adapt and enhance existing structure and function, what he appears to have in mind is a functional arrangement not unlike the subsumption architecture proposed by Rodney Brooks (1991), whereby simpler, specific reflex responses are modulated or suppressed by higher “reflexes” that reflect more general sensory-motor coordination. It is, in any case, clear that Ramon y Cajal imagined overall brain function was achieved via the establishment of a hierarchical continuum of sensorimotor control processes, all aimed at “conferring advantage in the struggle for survival” (Ramon y Cajal 1904/1995, p. 17).

1.4 Embodied Cognition

As noted above, functionalism was something like the orthodoxy in American psychology until the 1950s, when the “cognitive revolution” happened. The cognitive revolution replaced the functionalist ideas with ideas drawn from the Cartesian, rationalist tradition. The idea that thinking is computation occurring within the brain runs counter to the functionalist focus on the place of thinking in action and in evolutionary context; it is also, at best, neutral with respect to cerebralism. The idea that thinking is computation encourages a lack of interest in the brain. This is the case because computational processes are multiply realizable, which is to say that the same computational processes can occur in many different media. The web browser Firefox, for example, can run in the Mac, Windows, and Linux operating systems and on very different computer hardware. Despite differences in implementation, it is, in an important sense, the same software. Similarly, the purported computational processes that implement, for example, face recognition can be implemented

differently in different brains, and could even be implemented on a computer, while still being the same software. This encouraged cognitive scientists to ignore details about the brain when they proposed computational mechanisms for cognition (e.g., Fodor, 1975). In doing so, they rejected the cerebralism of the functionalist tradition. At the same time, computational cognitive science abstracted away from the details of action and bodily control. If cognition is a computational process, it is natural to treat the body as a mere peripheral device, like keyboard or modem, that provides information about the environment to the central processor that does the real cognitive work. Completing the rejection of the functionalist tradition is the antipathy that many of the founders of cognitive science have shown to evolution by natural selection. Infamously, Chomsky argued that the human language facility could not have evolved by natural selection (Chomsky, 1988). More recently, Jerry Fodor has gone from arguing that evolution by natural selection cannot explain how thoughts have meaning (1990) to arguing that evolution by natural selection cannot explain the nature of cognition (2000) to arguing that evolution by natural selection is simply ill-conceived (2007).

In the 1980s, psychology began to reclaim its functionalist foundations. As Bechtel, Abrahamsen, and Graham (1999, p. 75) put it, cognitive science moved “outwards into the environment and downwards into the brain.” The movement downwards into the brain was sparked by the introduction of drastically improved neural imaging techniques—including the introduction of positron emission tomography (PET) in the late 1970s (Sokoloff et al., 1977) and functional magnetic resonance imaging (fMRI) in the early 1990s (Ogawa, Lee, Kay, & Tank 1990)—and with the renaissance of artificial neural network modeling (Rumelhart, McClelland & PDP Research Group, 1986). These innovations allowed cognitive scientists and psychologists to focus in on the details of neural activity, at the same time strongly suggesting that these details really do matter. With the rise to prominence of cognitive neuroscience in the 1980s, Jamesian cerebralism was back. The simultaneous move outwards into the environment was initiated by the publication of Gibson’s posthumous *The Ecological Approach to Visual Perception* (1979), especially its more widely available second edition (1986). Gibson argued that the primary function of perception is the guidance of action, and because of that, the primary perceivables are affordances, or opportunities for action. From this strongly evolutionary perspective, the object of psychological inquiry was not the brain as computer, but rather perceptual systems—which include the brain, sensory surfaces, and moving body of an animal—surrounded by their information-rich environments. Gibson’s view was an explicit reclamation of the functionalist focus on evolution and the role of perception and cognition in controlling action.

In many ways, however, the real beginning of the movement known as “embodied cognition” came a few years later in the form of Rodney Brooks’s “Intelligence without representation” (1991). In that paper, Brooks used an explicitly evolutionary argument to shift the focus of cognitive science from abstract thinking to the control of action. Brooks presented a timeline of evolutionary highlights, from the appearance of single-celled organisms approximately 3.5 billion years ago, to the appearance of vertebrates approximately 500 million years ago, to the advent of written language about 5,000 years ago. Though the intervening decades have revised some of these dates, Brooks’s point stands. As he put it, the majority of evolutionary “research and development” was spent on getting from single-celled organisms to

vertebrates, which is to say getting from living things to creatures with sophisticated control of their actions. From this, Brooks concludes that the bulk of intelligence is perception and action, with language and other human-specific abilities mere icing on the cake.

The movement that followed was a restoration of Jamesian functionalism and rejection of the abstraction away from the brain and the body which came with the cognitive revolution. The details about the way the brain works *are* important to understanding cognition; cognition and the brain must be understood in their evolutionary context. In this evolutionary context, it is clear that for most of the history of life on earth, the primary function of nervous systems has been the control of action (e.g., Anderson, 2003; Barrett, 2011; Chemero, 2009; Clark, 1997). The current work in embodied cognitive science that arose from these sources (among many others) is broad-based, incorporating work in robotics, simulated evolution, developmental psychology, perception, motor control, cognitive artifacts, phenomenology, and, of course, theoretical manifestos. Given this variety of subject matter, there is also variety in theoretical approach. The following tenets, though, are more or less universally held among embodied cognitive scientists.

1.4.1 Interactive Explanation and Dynamical Systems

Explaining cognitive systems that include aspects of the body and environment requires an explanatory tool that can span the agent–environment border. Many embodied cognitive scientists use dynamical systems theory. That is, many (though not all) proponents of embodied cognitive science take cognitive systems to be dynamical systems, best explained using the tools of dynamical systems theory. A dynamical system is a set of quantitative variables changing continually, concurrently, and interdependently in accordance with dynamical laws that can, in principle, be described using equations. To say that cognition is best described using dynamical systems theory is to say that cognitive scientists ought to try to understand cognition as intelligent *behavior* and to model intelligent behavior using a particular sort of mathematics, most often sets of differential equations. Dynamical systems theory is especially appropriate for explaining cognition as interaction with the environment because single dynamical systems can have parameters on each side of the skin. That is, we might explain the behavior of the agent in its environment over time as coupled dynamical systems, using something like the following equations from Beer (1995):

$$\begin{aligned}\dot{X}_A &= A(X_A; S(X_E)) \\ \dot{X}_E &= E(X_E; M(X_A))\end{aligned}$$

where A and E are continuous-time dynamical systems, modeling the animal and its environment, respectively, and $S(x_E)$ and $M(x_A)$ are coupling functions from environmental variables to animate parameters and from animate variables to environmental parameters, respectively. It is only for convenience (and from habit) that we think of the organism and environment as separate; in fact, they are best thought of as forming just one nondecomposable system, U . Rather than describing the way external (and internal) factors cause changes in the organism's behavior, such a model would explain the way U , the system as a whole, unfolds over time.

1.4.2 Changing the Role of Representations

Although embodied cognitive science's main modeling tool, dynamical systems theory, is neutral about mental representations, with few exceptions embodied cognitive scientists are representationalists. The representations they call on are indexical-functional (Agre and Chapman, 1987), pushmi-pullyu (Millikan, 1995), action-oriented (Clark, 1997), emulator (Churchland, 2002; Grush, 1997, 2004), or guidance representations (Anderson & Rosenberg, 2008). Action-oriented representations differ from representations in earlier computationalist theories in that they necessarily represent things in a nonneutral way, as geared to an animal's actions, as affordances. Action-oriented representations are more primitive than other representations, in that they can lead to effective behavior without requiring separate representations of the state of the world and the cognitive system's goals. That is, the perceptual systems of animals need not build an objective representation of the world, which can then be used by the action-producing parts of the animal to guide behavior; instead, the animal produces representations that are geared from the beginning toward the adaptive actions it aims to perform.

1.4.3 Intelligent Bodies, Scaffolded Environments, Fuzzy Borders

Given this minimized role of mental representation, it is a challenge to explain complex, intelligent behavior. In embodied cognitive science, some intelligence is "off-loaded" from the brain to the body and environment. As Ramon y Cajal noticed more than a century ago, our bodies are well-designed tools, making the jobs of our brains much easier. For example, our kneecaps limit the degrees of motion possible in our legs, easing balance and locomotion. It is only a small exaggeration to say that learning to walk is easy for humans because our legs already know how (see Thelen & Smith, 1994 and Thelen, 1995). This off-loading goes beyond the boundaries of our skin: The natural environment is already rich with affordances and information that can guide behavior. In interacting with and altering this environment, as beavers do when they build dams, animals enhance these affordances. Kirsh and Maglio (1994, see also Kirsh, 1995) show that manipulating the environment often aids problem solving. Their example is of Tetris players rotating zoids on-screen, saving themselves the work of mental rotation. Hutchins (1995) shows that social structures and well-designed tools allow humans to easily accomplish tasks that would otherwise be too complex. Many of us therefore believe that cognitive systems are not confined to the brain or body, but include aspects of the environment (Anderson, Richardson, & Chemero, 2012; Clark, 1997; Hutto, 2005; Hutto & Myin, 2012; Menary, 2007; Rowlands, 2006). Clark even argues (2003) that external tools including phones, computers, language, and so on are so crucial to human life that we are literally cyborgs, partly constituted by technologies. Echoing Ramon y Cajal's view of the sense organs, embodied cognitive scientists argue that the functional relationships that enable intelligent action are not among merely neural components, but instead integrate neurons, bodies, and environment.

These tenets of embodied cognition, of course, have consequences for the functional organization of the brain. We consider these in the next section.

1.5 Embodied Cognition and the Brain

In light of the discussion above, we would like to suggest three principles that together define a functionalist neuroscience. A functionalist believes that (1) the functional architecture of the brain has been established by natural selection and, more particularly, via a process marked by both functional differentiation and continuity; (2) our complex and diverse behavioral repertoire is supported primarily by the brain's ability to dynamically establish multiple different functional coalitions, coordinating both neural partnerships and external resources; and (3) the brain is fundamentally action-oriented, with its primary purpose to coordinate the organism's ongoing adjustments to external circumstances.

Despite the growing interest in, and information about, the details of neural processing, much of the cognitive neuroscience of the last two decades has still been guided by cognitivist principles and the computer metaphor for the brain (see Miller, 2003 and Posner, Petersen, Fox, & Raichle, 1988 for discussion). Thus, a truly functionalist cognitive neuroscience has yet to emerge. There is, however, some suggestive work that points the way.

1.5.1 Brains Evolve through Elaboration

Consider the first principle, that the functional architecture of the brain should reflect an evolutionary history marked by both functional differentiation and also the incorporation and reuse of existing structures for new purposes. If the last century of neuroscience has established anything, it is that the various regions of the brain are functionally differentiated. For most of that time, this fact has been taken to indicate that each region of the brain is highly functionally specialized, implementing a single cognitive operation (e.g., Posner et al., 1988 and Kanwisher, 2010). Recent work, however, has characterized brain regions in a multi-dimensional manner that highlights functional differences while recognizing that, in point of fact, each region of the brain appears to be active in multiple diverse circumstances (Anderson, Kinnison, & Pessoa, 2013; Hanson & Schmidt, 2011; Poldrack, Halchenko, & Hanson, 2009).

Indeed, it is at this point well established that individual regions of the brain support many different tasks across multiple task categories, as would be predicted by the principle of continuity. For instance, although Broca's area has been strongly associated with language processing, it turns out to also be involved in many different action- and imagery-related tasks, including movement preparation (Thoenissen et al., 2002), action sequencing (Nishitani, Schürmann, Amunts, & Hari, 2005), action recognition (Decety et al., 1997; Hamzei et al., 2003; Nishitani et al., 2005), imagery of human motion (Binkofski et al., 2000), and action imitation (Nishitani et al., 2005; for reviews, see Hagoort, 2005; Tettamanti & Weniger, 2006). Similarly, visual and motor areas—long presumed to be among the most highly specialized in the brain—have been shown to be active in various sorts of language processing and other “higher” cognitive tasks (Damasio & Tranel, 1993; Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996; Glenberg & Kaschak, 2002; Hanakawa et al., 2002; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995; Martin, Wiggs, Ungerleider, & Haxby, 1996; Martin, Ungerleider, & Haxby, 2000; Pulvermüller, 2005; see Schiller, 1996 for a related discussion). Excitement over the discovery of the fusiform face

area (Kanwisher, McDermott, & Chun, 1997) was quickly tempered when it was discovered that the area also responded to cars, birds, and other stimuli (Gauthier, Skudlarski, Gore, & Anderson, 2000; Grill-Spector, Sayres, & Ress, 2006; Rhodes, Byatt, Michie, & Puce, 2004; Hanson & Schmidt, 2011).

Recent meta-analyses of neuro-imaging results have tended to support this emerging picture of a functionally differentiated, but not functionally specialized, brain. For example, Russell Poldrack (2006) estimated the selectivity of Broca's area by performing a Bayesian analysis of 3,222 imaging studies from the BrainMap database (Laird, Lancaster, & Fox, 2005). He concluded that current evidence for the notion that Broca's area is a "language" region is fairly weak, in part because it was more frequently activated by nonlanguage tasks than by language-related ones. Similarly, several whole-brain statistical analyses of large collections of experiments from BrainMap (Laird et al., 2005), Neurosynth (Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011), and other sources demonstrate that most regions of the brain—even fairly small regions—appear to be activated by multiple tasks across diverse task categories (Anderson, 2010; Anderson et al., 2013; Anderson & Penner-Wilger, 2013).

That this apparent functional diversity is a reflection of the evolutionary history of the brain is supported by some interesting features of the *pattern* of use and reuse of individual regions of the brain across multiple circumstances. For instance, it appears that, *ceteris paribus*, older regions of the brain tend to be used in more tasks—presumably because they've been around for longer, and have thus had more opportunity to be incorporated into multiple functional coalitions (Anderson 2007). In addition, more recently emerged cognitive functions, such as language, appear to be supported by more and more widely scattered brain regions than do evolutionarily older functions such as vision and attention (Anderson, 2010; Anderson & Penner-Wilger, 2013). Again, this makes sense in light of both differentiation and continuity, for the later a given cognitive process or behavioral competence emerges, the greater the number and diversity of neural structures that will be available to support the new competence, and there is little reason to expect structures with the necessary functional properties will always be near one another in the brain.

1.5.2 Cognition Does Not Respect Boundaries

This brings us to the second principle, that achieving behavioral competence is a matter of establishing the right functional coalitions to support the tasks in question. There is little work that specifically investigates the neural supports for the incorporation of external resources into cognitive processing. Just as we create physical tools like hammers, knives, and levers to augment our physical capacities, so too we have invented cognitive artifacts to augment our mental ones, perhaps none more important than the written symbols and other tokens we manipulate in mathematical processing. And we *do* manipulate and interact with them as tools: we write them, move them, strike them out, gesture at and over them. How we marshal the internal resources of memory and perception along with the external resources of pencil, paper, and space to solve mathematical problems is a sensorimotor skill that is very poorly understood behaviorally, and not at all neuroscientifically (Clark, 1997; Landy & Goldstone, 2009). This is a lacuna that the field should begin to address.

However, there is certainly evidence that, *within* the brain, cognitive function is a matter of flexibly assembling the right coalition of neural partners. Some suggestive evidence for this possibility comes from a meta-analysis of more than 1100 neuroimaging studies across 10 task domains: It was demonstrated that, although many of the same regions of the brain were used and reused in multiple tasks across the domains, the regions cooperated with one another in different patterns in each task domain (Anderson & Penner-Wilger, 2013).

Experimental work investigating temporal coherence in the brain also points in the direction of large-scale modulation of neural partnerships in support of cognitive function. For instance, there is evidence relating changes in the oscillatory coherence between brain regions (local and long-distance) to sensory binding, modulation of attention, and other cognitive functions (Varela, Lachaux Rodriguez, & Martinerie, 2001; Steinmetz et al., 2000). Two early findings illustrate the basic notion well: Friston (1997) demonstrated that the level of activity in posterior parietal cortex determined whether a given region of inferotemporal cortex was face-selective, that is, its functional properties were modulated by distributed neural responses. Likewise, McIntosh et al. (1994) investigated a region of inferotemporal cortex and a region of prefrontal cortex that both support face identification and spatial attention. McIntosh et al. showed that during the face-processing task the inferotemporal region cooperated strongly with a region of superior parietal cortex; while during the *attention* task, that same region of parietal cortex cooperated more strongly with the prefrontal area. Similar patterns of changing functional connectivity are observed over developmental time, which suggests that acquiring new skills involves changes to both local and long-distance functional partnerships (Fair et al., 2009; Superkar, Musen, & Menon 2009). It seems reasonable to predict that such results will continue to emerge, given the increasing interest in network-oriented approaches to the brain (Sporns, 2011).

1.5.3 Brains Function to Guide Adaptive Action

Finally we consider the third principle, that the brain should be understood as an action-oriented system. It is here, perhaps, that there is the most work left to be done to establish a functionalist neuroscience: The computer metaphor for the brain still dominates the cognitive neurosciences, leading researchers to interpret the neural activity observed during experiments as reflecting information processing, rather than action coordination (but see Anderson, 2015). It is nevertheless worth highlighting one recent line of work in the neural bases of decision making, to illustrate what a more action-oriented approach to the brain might look like.

Prevailing models of decision making have generally inherited from the cognitivist approach to the mind the notion that decision making involves first building an objectively specified world-model, then generating possible action plans, deciding between them (action selection), and finally determining how the motor system will enact them (action specification). But, as we saw above, from the functionalist embodied perspective, perception naturally assesses the adaptive values of current organism–environment relationships and detects opportunities for changing those values through action. If we perceive the world in terms of the opportunities for action that it affords, then deciding what to do might be largely a matter of

choosing which perception–action path—which affordance—has the highest predicted return.

The proposal made here is that *the process of action selection and specification occur simultaneously* and continue even during overt performance of movements. That is, sensory information arriving from the world is continuously used to specify currently available potential actions... From this perspective, behaviour is viewed as a constant competition between internal representations of the potential actions which Gibson (1979) termed ‘affordances’. Hence, the framework presented here is called the “affordance competition hypothesis.” (Cisek, 2007, p. 1586)

Although it is imprecise to talk of “representing” affordances—an affordance is the perceivable relationship between an organism’s abilities and features of the environment (Chemero, 2003; 2009)—clearly it is the notion of internal (neural) competition between possible courses of action that is the center of Cisek’s account. There are two central tenets to his hypothesis, both of which fit in nicely with the functionalist approach to the brain being described here:

- 1 **The process of action selection and specification occur continuously and in parallel.** Because the organism’s brain evolved to support interactive behavior, and perception is to be understood in terms of the detection of opportunities for action, it stands to reason that the process of selecting and specifying actions is a continuous, ongoing part of simply perceiving and acting in the world. Elaborating this notion, Cisek and Kalaska (2010) write:

Schmolecky et al. (1998) showed that neural responses to simple visual tasks appear quickly throughout the dorsal visual system and engage putatively motor-related areas such as FEF [frontal eye fields] in as little as 50ms. This is significantly earlier than some visual areas such as V2 and V4. ... In a reaching task, population activity in PMd responds to a learned visual cue within 50ms of its appearance (Cisek & Kalaska 2005). Such fast responses are not purely visual because they reflect the context within which the stimulus was presented. For example, they reflect whether the monkey expects to see one or two stimuli (Cisek & Kalaska 2005), reflect anticipatory biases or priors (Coe et al. 2002; Takikawa et al. 2002), and can be entirely absent if the monkey already knows what action to take and can ignore the stimulus altogether (Crammond & Kalaska 2000). In short, these phenomena are compatible with the notion of a fast dorsal specification system that quickly uses novel visual information to specify the potential actions most consistently associated with a given stimulus (Gibson 1979; Milner & Goodale 1995). (Cisek & Kalaska, 2010, p. 285)

- 2 **For any given behavior, both processes occur in the same regions of the brain.** Regional differentiation in the brain reflects different capacities for managing certain classes of sensorimotor transformation, rather than (for instance) specializations for perceptual discrimination, decision making, and action execution. Cisek and Kalaska (2010) write:

Studies on the neural mechanisms of decision making have repeatedly shown that correlates of decision processes are distributed throughout the brain, notably

including cortical and subcortical regions that are strongly implicated in the sensorimotor control of movement. Neural correlates of decision variables (such as payoff) appear to be expressed by the same neurons that encode the attributes (such as direction) of the potential motor responses used to report the decision, which reside within sensorimotor circuits that guide the online execution of movements. These data and their implications for the computational mechanisms of decision making have been the subject of several recent reviews (Glimcher 2003; Gold & Shadlen 2007; Schall 2004). (Cisek & Kalaska, 2010, p. 270)

This overlap has behavioral consequences that are hard to explain within the classical framework. For instance, one body of evidence shows that the trajectory of reaching movements depends on the amount of separation of the targets in space: Subjects move directly to the chosen target when the options are far apart, but initially reach between the targets when they are close together, and only later veer to their selection (Ghez et al., 1997). Such behavior is naturally explained as a side-effect of the similarity of the response options in the case of the close targets; the nearly identical neural patterns generated by the similar affordances will tend to reinforce one another, perhaps even merging for a time, and it is only when the differences in the reach trajectory between the options become more pronounced as the hand approaches the targets that the two possibilities become distinguishable and competitive (Cisek, 2006; Erlhagen & Schöner, 2002). Similarly, when subjects in two alternative forced choice tasks are asked to indicate their decision by moving a hand or a cursor to the chosen location, the subject's confidence in their choice predicts aspects of their movement of including endpoint and peak velocity (McKinstry et al., 2008). Cisek and Kalaska (2010) conclude:

These findings are difficult to reconcile with the idea that cognition is separate from sensorimotor control (Fodor 1983) but make good sense if the continuous nature of the representations that underlie the selection of actions has been retained as selection systems evolved to implement increasingly abstract decisions. (Cisek & Kalaska, 2010, p. 283)

This perspective illustrates not just the notion of cognitive continuity, but also the potential power of action-oriented representations in interpreting neuroscientific data. If brains are action-oriented systems, then whatever representations it trucks in should reflect this functional inheritance. Cisek believes that the decision-making literature points in precisely this direction:

The affordance competition hypothesis ... differs in several important ways from the cognitive neuroscience frameworks within which models of decision making are usually developed. Importantly, it lacks the traditional emphasis on explicit representations which capture knowledge about the world. For example, the activity in the dorsal stream and the fronto-parietal system is not proposed to encode a representation of objects in space, or a representation of motor plans, or cognitive variables such as expected value. Instead, it implements a particular, functionally motivated mixture of all these variables. From a traditional perspective, such activity appears surprising because it does not have any of the expected

properties of a sensory, cognitive or motor representation. It does not capture knowledge about the world in the explicit descriptive sense expected from cognitive theories and has proven difficult to interpret from that perspective... However, from the perspective of affordance competition, mixtures of sensory information with motor plans and cognitive biases make perfect sense. Their functional role is not to describe the world, but to mediate adaptive interaction with the world. (Cisek, 2007, p. 1594)

For a functionalist neuroscience to fully emerge, this action-oriented perspective must be taken up into every corner of the field. Given the apparent challenges facing the current framework, and the importance of integrating the study of the mind and brain more fully with the ecological and evolutionary biology, this is a possibility we should both welcome and encourage (Anderson, 2010; 2015; Anderson, Richardson, & Chemero 2012).

1.6 Conclusion

Our point in this chapter has been that a focus on evolution in psychology and neuroscience has to come with a focus on action. Our hominid predecessors were able to walk, run, forage, and avoid predators, but were presumably not able to do logic or read. The brain evolved to guide action, not write sonnets. This fact has consequences for how one does both psychology and neuroscience. We have pointed to 20th-century functionalist traditions in psychology and neuroscience where action has, indeed, been the focus. The rejuvenation of functionalism in psychology, via the embodied cognition movement, is beginning to be carried over into the neurosciences. Future neuroscience has to take our evolutionary history into account, and, to do so, it must become more action-oriented.

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