Seeking Synthesis: Language as an Integrated System

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Abstract

We discuss two problems for a general scientific understanding of language, sequences and synergies: how language is an intricately sequenced behavior and how language is manifested as a multidimensionally structured behavior. Though both are central in our understanding, we observe that the former tends to be studied more than the latter. We consider very general conditions that hold in human brain evolution and its computational implications, and identify multimodal and multiscale organization as two key characteristics of emerging cognitive function in our species. This suggests that human brains, and cognitive function specifically, became more adept at integrating diverse information sources and operating at multiple levels for linguistic performance. We argue that framing language evolution, learning, and use in terms of synergies suggests new research questions, and may be a fruitful direction for new developments in theory and modeling of language as an integrated system.

1. Introduction: Sequence and Synergy

Among the general aspects of language demanding explanation, there are at least two that seem especially puzzling. The first is about how language manifests as intricately *sequenced* behavior. The second is how language is manifested as a *multidimensionally structured* behavior. Both are important, but the first has tended to receive more attention in the cognitive sciences.

The first of these was famously described by Lashley (1951) as the problem of the serial order of behavior. Human and non-human behavior is often complex and hierarchically organized in time. This is especially true of human language. Lashley's problem may have its starkest exhibit in syntax. Syntax has figured centrally in cognitive science up to the present, with recent renewed attempts at consecrating recursion (Hauser, Chomsky, & Fitch, 2002; Watumull, Hauser, Roberts, & Hornstein, 2013). Similarly, such a concern with sequential structure extends from sounds to meanings, too.

The second aspect of language — the multidimensionality of its performance — is how any instance of natural language is a coherent assemblage of quite an array of different behaviors, at different levels of measurement. This aspect has received less attention: How do syntax and other levels work together during natural linguistic performance, and how does the human cognitive system integrate diverse sources of information to support complex linguistic processes *in situ*? In some domains of cognitive science, many processes interacting as a coherent system are referred to as a *synergy*. We will use "synergy" in a more casual sense here, though it has more formal definitions in other domains (for a recent discussion see Riley, Richardson, Shockley, & Ramenzoni, 2011).

With regard to the first puzzling aspect of language, significant progress has been achieved. For example, there seem to be countless potential solutions to syntax. These many competing solutions have been on offer for many years, and some have even found their way into impressive applied natural language processing. Put simply, there are lots of good ideas about how to figure out syntax, *in particular*.

With regard to the second aspect, much less progress has been achieved. Human language can be seen as a very complex kind of synergy: Many processes operate simultaneously in concert during any bout of linguistic performance. The problem of understanding this coherent performance is a problem of understanding synergies. As we elaborate below, the direction of human brain evolution, and the abstract computational abilities that emerge from a particular neural organization, seem highly suitable to support linguistic synergies.

Admittedly, in linguistics and psycholinguistics, concern for interfacing levels has been around for some time, and made prominent more recently, for example, by Jackendoff (2003). Jackendoff expresses chagrin with the focus on individual levels, in particular syntax (labeling it "syntactocentrism"), and he articulates the need to interface levels gracefully in our theories of human language. There is a growing literature on bridge principles for linguistic levels (see Ramchand & Reiss, 2007). More broadly, an integrative strategy can also be found in construction grammar and cognitive linguistics (Croft & Cruse, 2004; Goldberg, 1995), and functionalist approaches in general, where syntax and other structural elements of language are not granted autonomy from the rest of the cognitive system. The interactive aspect of speech has already been explored in terms of synergies (Kelso, Tuller, Vatikiotis-Bateson, & Fowler, 1984), showing the rapid interaction and adaptation of phonological knowledge and articulatory mechanisms (see also Fusaroli, Rączaszek-Leonardi, & Tylén, 2012 for discussion of discourse).

This problem — discerning core principles of language as an integrated system — is completely unsolved. Despite these threads of research in the language sciences, this *integrative* problem seems still to receive less attention than the more common strategy of isolating and investigating one or just a few levels. This brief review and discussion takes for granted that the problem is both broad and scientifically viable. Solving the puzzle could lead to interesting computational generalizations that relate to language and other human cognitive achievements. These generalizations would contribute to understanding how and why language evolved to become so "texturally" complex. The following two sections consider the problem in very general, theoretical terms. Much as research on syntax may look to abstract notions from, for example, computing theory (e.g., Watumull et al., 2013), we consider very general, and sometimes abstract, conditions that would hold in brain evolution and the computational implications of these conditions. We begin with some general features of human brain evolution.

2. Human Brain Evolution

Although the human brain is particularly large — about three times larger than it should be for a primate of our body size — it may not just be a bigger version of a standard primate brain, but may be different in interesting ways (Schoenemann, 2006). Some, but not all, of these interesting differences are predictable consequences of nonlinear brain scaling effects. One interesting nonlinear scaling effect is the degree to which connectivity between cortical areas changes with increasing brain size. Although larger brains do have many more axonal connections between brain areas than smaller brains, the increase does not keep pace with the increase in gray matter (Ringo, 1991).[1]

This means not only that cortical areas tend to become larger (presumably supporting more complex processing), but also that given areas appear to be less directly interconnected than in smaller brains. The effect of this is to increase the degree to which processing can occur in any given area partly independently of other areas (depicted in Fig. 1). Based on mammalian scaling trends, human brains are predicted to have ~50% more areas than do chimpanzees (Changizi & Shimojo, 2005). Additionally, in fMRI studies of resting state and natural vision, brain activation in humans and monkeys may reveal unique network combinations in human brains (Mantini, Corbetta, et al., 2013).
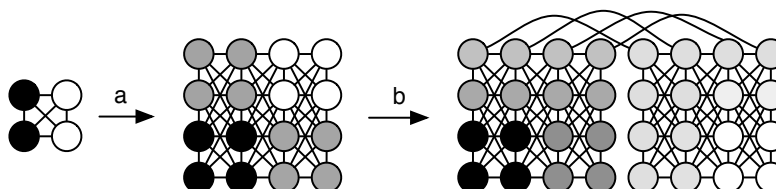

Figure 1: With wiring costs amidst increasing size, functional gradients emerge (a). With increasing size and more reliance upon experience-dependent organization, diverse patterns of interconnections may support segregation of functional gradients and their integration (b). Molecular gradients that can force input specialization (black/white) by areas, in the leftmost network, may not sustain this specialization with increases in the cortical sheet (Buckner & Krienen, 2013), and so multisensory regions form functional but interactive clusters.

Human brain evolution appears to have specifically emphasized the expansion of areas that integrate different kinds of information — so-called "association" areas — rather than areas that focus solely on single modalities or highly restricted types of information (Buckner & Krienen, 2013; Nieuwenhuys, 1994; Schoenemann, 2012). In fact, it has been argued that the neocortex is mostly multisensory, and that even within "unisensory" areas there is substantial evidence of input from other senses. For example, there is visual and somatosensory processing in auditory areas, and auditory and somatosensory processing in visual areas (Ghazanfar & Schroeder, 2006). Additionally, it appears that white matter increases have been particularly emphasized in prefrontal regions (Schoenemann, 2006), indicating that there has been an emphasis on connecting this area with other regions.

Human brain evolution (and perhaps encephalization in general) thus shows a kind of "segregation with integration" pattern: increasing cortical regions that serve as computational clusters, but are sustained by widespread information exchange (cf. Tononi & Edelman, 1998). Because conceptual understanding appears to be instantiated in the brain as networks of activation connecting differing brain regions (Barsalou, 2008), greater numbers of cortical areas connected in increasingly complicated ways likely leads to an increase in the richness, subtlety, and complexity of conceptual understanding in human brains (Schoenemann, 2012; see also Deacon, 1998).

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[1] It is important to note that there is some debate about our body-relative brain size (Herculano-Houzel, 2009). Using the same methods that seem to suggest we simply have a linearly-scaled primate brain, the observation we make here about white matter has also been supported: Gray matter scales differently relative to white matter, and small-world connectivity in white matter allows sustained local connectivity but with distributed long-range connectivity (Herculano-Houzel et al., 2010).

These brain changes have also had the effect of magnifying the importance of learning and memory. There is a strong positive relationship between brain size and total maturation time in primates (Harvey & Clutton-Brock, 1985). Although larger brains tend strongly to be found in larger bodied primates, the relationship between brain size and maturation time is not just a simple effect of larger bodies taking longer to develop. For example, humans take about 2.5 times longer to reach maturity than do gorillas, even though adult gorillas weigh 2 to 3 times as much in overall body mass (data from: Harvey & Clutton-Brock, 1985). By contrast, humans have brains about 2.5 times larger. The reason larger brains are associated with longer periods of maturation is that brain networks depend critically on experiential input for their development (Hrvoj-Mihic, Bienvenu, et al., 2013). This means that the social environment is particularly influential in brain development. This evolutionary effect may be enhanced if subtle motivational changes in humans enhanced reward signals from social co-presence (e.g., Syal & Finlay, 2011).

There is disagreement whether all these changes can be predicted as linear scaling from primate brains (Herculano-Houzel, 2009), or some other developmental scaling from a mammalian template, rather than specialized modifications (e.g., Workman et al., 2013). However, the general observations about small-world interconnectivity because of white-to-gray-matter scaling, and pervasive multisensory processing in brain areas, seems to be widely accepted. In sum, the human brain displays a pronounced scaling of functional diversification of multisensory information integration. Local network processing is integrated over longer and longer ranges of circuitry. There may be general computational implications of this scaling, as the human brain/body/environment system operates across many levels.

3. Computational Implications of Multiscale, Multimodal Dynamics

Our review thus far raises the question of how the evolved structural properties of human brains give rise to their remarkable flexibility in integration and cognitive function. This question can be cast in terms of the kinds of complex synergies that human brains afford, as scaffolds on already social primate brains and behaviors (and, in humans, perhaps considerably more so: *inter alia*, Syal & Finlay, 2011; Hermann et al., 2007).

Here we briefly develop an answer to this question by thinking about synergies in general terms. Consider, for example, the idea of "relative coordination" of von Holst (1939/73), which illuminates a fundamental principle of synergies. von Holst (1939/73) studied locomotion in centipedes and other organisms. He was interested in how centipede limbs coordinate to crawl. One possibility is that fixed movement patterns originate in the genome, and are parameterized so they can be expressed under various conditions (see Duysens & Van de Crommert, 1998 for discussion). von Holst demonstrated a major challenge to this approach. He amputated limbs from centipedes so that their crawl pattern would not work for locomotion. Nonetheless, crippled centipedes readily produced a new crawl pattern with their remaining legs.

von Holst offered relative coordination as an alternative to genetically encoding particular movement patterns. Limbs are drawn into particular *interdependent* rhythmic relationships in pursuit of a "goal" (also see Kelso, 1995). This balance is theorized to allow for qualitatively different patterns to emerge under a wide range of different locomotive conditions, and dynamics should naturally follow an energy gradient to settle on efficient patterns given certain conditions (Van Den Berg, 2000).

This balance among components to preserve function — in spite of almost uncountable possible perturbations — is necessary for living things in labile worlds. Flexibility in generating patterns may be essential, and tied to the "segregation with integration" evolutionary pattern just discussed. Balancing these complementary forces can foster pattern flexibility, as supported by work on the dynamics of component interactions in broad classes of complex systems. Indeed it has been hypothesized that living systems "try" to remain hovering at the juncture points between segregation and integration ("critical points"; Bak, 1996), particularly by virtue of being composed of elements at multiple scales (Moretti & Muñoz, 2013).

The balancing of component interactions is hypothesized to underlie not only the multiscale nature of living systems, but also their memory and computational capacities. Patterns of activity have memory to the extent that they hold information about past states of the systems they're embedded in. Because these systems have structure at different spatial scales (e.g., neurons to neuronal groups), they

also have structure at different temporal scales. Changes across the system can be sustained at a longer time scale as that system accumulates its local transient fluctuations which, in turn, are constrained by that longer time scale of accumulation (Van Orden et al., 2013). Put differently: Activation across levels is mutually interdependent, and can preserve residual information that could be put to use for generating sequences of cognition or behavior. One promising related avenue for neural modeling is *reservoir computing*, which refers to a theoretical framework in which functions of memory and computation are extracted from systems whose dynamics are inherently nonlinear and recurrent (Maass, Natschlager, & Markram, 2002). Interestingly, studies have shown that dynamics giving rise to the kind of "balancing" we just described also maximize their memory and computational capacities (Bertschinger & Natschlager, 2004; Kello, 2013). These studies suggest that principles giving rise to multiscale living systems might also give rise to relatively maximized properties of memory and computation.

In slightly different terms, systems like brains operate over multiscale dynamics. Perhaps the most compelling neurally-inspired models of computation have these properties (Grossberg, 2000; Izhikevich & Edelman, 2007; Kello, 2013). If it is true that scaling properties of the growing cortical sheet made this pattern of organization more pronounced, as reviewed in Section 2, it suggests conditions were appropriate for a radical increase in cognitive abilities. Synergies among modalities and scales may bring about new cognitive functions.

4. Next Steps for Synergies in Language

The potential for deep relationships among development, cognition, and language has been a point of heated debate in cognitive science (e.g., Christiansen & Chater, 2008). Though we have advocated that language can be based on core computational principles inherent in multiscale and multimodal neural organization, this idea alone obviously does not "explain" language. Any theory of language origins and change must distinguish itself, in some way, from more fundamental properties of all organisms — all organisms face problems of coordinating with a complex environment. But the same may be said of the first puzzle that began this paper. Recent proposals for the centrality of recursion take recourse to similarly abstract principles, such as computing theory (e.g., Watumull et al., 2013). In the same way that these proposals look to such general principles, it may be fruitful to consider how the general principles of multiscale systems "build linguistic synergies" (cf. Deacon, 2011; Juarrero, 1999).

We considered what may be a crucial ingredient in language evolution: multimodal synergy. Any bout of verbal behavior marshals a broad suite of neural subsystems, amid environmental constraints, that converge to systematically shape the behavior of a speaker and listener. Language is driven by a coordination problem that is specific to our ecology, and is achieved by placing in a relationship of interdependence a wide array of modalities (both in the sense of sensory and motor modality, and in the sense of "informational level"). This notion does not exclude other proposed aspects of language evolution, and may support numerous pre-adaptations (Hurford, 2003, offers a great review of pre-adaptations).

Multimodal and multiscale organization may not be just a contingent feature of a brain with language, but a necessary feature of a brain that has language. Perhaps that organization is conditionally sufficient, too, assuming phylogenetic pre-cursors for social behavior. The upshot is that language seems to recruit all kinds of subsystems for communicating meaning (Anderson, 2010); by watching just one minute of interaction, one sees the cascading recruitment of levels from eyes to dialog moves (Louwerse, Dale, Bard, & Jeuniaux, 2012). In many respects this is not a new proposal. For example, Carruthers has referred to language as a kind of cognitive-intersection system (Carruthers, 2002). Elman has pointed to language emergence as a kind of "conspiracy theory" of many interacting constraints (Elman, 1999; see also, among many others, MacWhinney, 1999; Seidenberg & MacDonald, 2001; "Five Graces Group" et al., 2009). In terms of multiscale organization, language-related patterns of activity can be found from individual spikes to system-wide patterns of activity (Giraud & Poeppel, 2012; cf. Anderson, 2010). Thus language processing does not appear to have a temporal or spatial scale in brains that is privileged. Instead, when it is happening, language is expressed as a very broad property of human brain activity.

But as noted above, multimodality in this broad sense can also be seen as a problem faced by many creatures. All organisms face these problems of coordination that seem computationally challenging. As we reviewed above, although the human brain appears to obey scaling laws within

primates, the manner in which primate brains can pack nerve cells, and the way that white matter may have restructured and selectively rewired epigenetically could have allowed (1) unusually extensive multimodal interconnectivity in a (2) very large brain in a (3) species with strong and stable social strategies. Space severely restricts our discussion here, so we opted to review general ideas about multimodal and multiscale basis for human linguistic synergies. But the approach also generates new questions and situates a wide variety of research in a new light. We highlight some of these potential research avenues and connect them to synergies in Table 1. Put differently: Given any linguistic level of analysis we are interested in, ultimately we must come to understand how natural verbal behavior involves a balance between this chosen level of analysis, and other aspects of language around it. We began this paper averring that this is also a fundamental aspect of language — constitutive of any natural act of language, however brief or laboratory ensconced.

We cannot, of course, propose any distinct solutions to these issues in so short a space. Some scientists of language are concerned with articulating the most economical and abstract description for some chosen aspect of language performance. This is an abstract goal, seeking core principles. A complementary goal, into which we hope to have infused some intrigue, is to engage in similarly abstract exploration of *integrated* systems — systems that are operating through many interdependent parts. This offers up the relatively abstract challenge to find the principles that underlie this interdependence, and understand its computational implications (cf. Mitchell, 2009, Chap. 19). These implications may very well be, for example, the core aspects of language, emerging from "conspiracies of constraints" (Elman, 1999).

Many proposed conditions of the prehominid line encourage tales of selection pressure for multimodality, such as complex social skill, capacious memory, and hierarchical organization. A provocative notion is that, quite different from Hauser et al. (2002), recursion may be seen as a consequence of a brain's ability to organize multiscale behavior in time, rather than recursion springing from its own unique adaptation (see Dominey, 2013 for suggestive modeling work).

Table 1: Research agendas and reinterpretation of some major areas of the language sciences in terms of dynamic interactions among modalities and scales.

Domain	Synergistic* "balancing act"	Examples of synergistic influences	Exemplary reference
perception	bottom-up and top-down integration to maximize signal over noise	integrating cues from visual and auditory sources	Ghazanfar & Takahashi, 2014
production	assembling muscle groups dynamically to maximize discriminability	muscles and neural control form stable lower-dimensional control structures	Gick & Stavness, 2014
conceptualization	binding information from radically different modalities	abstraction relates to understanding at more concrete levels	Barsalou, 2008
sentential meaning	integration of different sources of information to infer meaning	interaction among cues can lead to radically altered judgments	Knobe, 2003
illocution	multiple realization of intention of meaning	radically different strategies to convey the same overall intention	Oller, 2004
discourse	stable goal-oriented communication	diverse indices signaling stable organization among pairs	Fusaroli et al., 2014
aphasias	recovery of function or compensatory strategies	brain reorganization, adoption of new discourse strategies	Hillis, 2007
composition	semantic (topical) stability with shifting diction / word choice	dynamics of topic shift will show aligned dynamics in word choice	Doxas et al., 2010

* "Synergistic" in that the overall stable balancing act is brought about by an interaction of multiple processes operating together

References

"Five Graces Group" et al. (2009). Language is a complex adaptive system. *Language Learning*, 59 (Suppl. 1), 1-27.

Anderson, M. L. (2010). Neural reuse: A fundamental organizational principle of the brain. *Behavioral and Brain Sciences*, *33*(04), 245-266.

Bak, P. (1996). *How nature works*. New York: Springer-Verlag.

Barsalou, L. W. (2008). Grounded cognition. *Annual Review of Psychology*, *59*, 617–45.

Bertschinger, N., & Natschlager, T. (2004). Real-time computation at the edge of chaos in recurrent neural networks. *Neural Computation*, *16*(7), 1413-1436.

Buckner, R. L., & Krienen, F. M. (2013). The evolution of distributed association networks in the human brain. *Trends in Cognitive Sciences*, *17*(12), 648-665.

Carruthers, P. (2002). The cognitive functions of language. *Behavioral and Brain Sciences*, *25*(6), 657–674.

Changizi, M. A., & Shimojo, S. (2005). Parcellation and area-area connectivity as a function of neocortex size. *Brain, Behavior and Evolution*, *66*(2), 88–98.

Christiansen, M. H., & Chater, N. (2008). Language as shaped by the brain. *Behavioral and Brain Sciences*, *31*(05), 489-509.

Croft, W., & Cruse, D. A. (2004). *Cognitive linguistics*. Cambridge University Press.

Deacon, T. W. (1998). *The symbolic species: The co-evolution of language and the brain*. WW Norton & Company.

Deacon, T. W. (2011). *Incomplete nature: How mind emerged from matter*. WW Norton & Company.

Dominey, P. F. (2013). Recurrent temporal networks and language acquisition—from corticostriatal neurophysiology to reservoir computing. *Frontiers in Psychology*, *4*.

Doxas, I., Dennis, S., & Oliver, W. L. (2010). The dimensionality of discourse. *Proceedings of the National Academy of Sciences*, *107*(11), 4866-4871.

Duysens, J., & Van de Crommert, H. W. A. A. (1998). Neural control of locomotion; Part 1: The central pattern generator from cats to humans. *Gait & Posture*, 7(2), 131-141.

Elman, J. L. (1999). The emergence of language: A conspiracy theory. In B. MacWhinney (Ed.), The *Emergence of Language* (pp. 1–27). Mahwah, NJ: Lawrence Erlbaum Associates.

Fusaroli, R., Rączaszek-Leonardi, J., & Tylén, K. (2014). Dialog as interpersonal synergy. *New Ideas in Psychology*, *32*, 147-157.

Ghazanfar, A. A., & Schroeder, C. E. (2006). Is neocortex essentially multisensory? *Trends in Cognitive Sciences*, *10*(6), 278–85.

Ghazanfar, A. A., & Takahashi, D. Y. (2014). The evolution of speech: vision, rhythm, cooperation. *Trends in cognitive sciences*, *18*(10), 543-553.

Gick, B., & Stavness, I. (2013). Modularizing speech. *Frontiers in psychology*, 4.

Giraud, A. L., & Poeppel, D. (2012). Cortical oscillations and speech processing: emerging computational principles and operations. *Nature Neuroscience*, *15*(4), 511-517.

Goldberg, A. E. (1995). *Constructions: A construction grammar approach to argument structure*. University of Chicago Press.

Grossberg, S. (2000). The complementary brain: Unifying brain dynamics and modularity. *Trends in Cognitive Sciences*, *4*(6), 233-246.

Harvey, P. H., & Clutton-Brock, T. H. (1985). Life history variation in primates. *Evolution*, *39*, 559–581.

Hauser, M. D., Chomsky, N., & Fitch, W. T. (2002). The faculty of language: What is it, who has it, and how did it evolve? *Science*, *298*(5598), 1569-1579.

Herculano-Houzel, S. (2009). The human brain in numbers: a linearly scaled-up primate brain. *Frontiers in Human Neuroscience*, *3*.

Herculano-Houzel, S., Mota, B., Wong, P., & Kaas, J. H. (2010). Connectivity-driven white matter scaling and folding in primate cerebral cortex. *Proceedings of the National Academy of Sciences*, *107*(44), 19008-19013.

Herrmann, E., Call, J., Hernández-Lloreda, M. V., Hare, B., & Tomasello, M. (2007). Humans have evolved specialized skills of social cognition: the cultural intelligence hypothesis. *Science*, *317*(5843), 1360-1366.

Hillis, A. E. (2007). Aphasia Progress in the last quarter of a century. *Neurology*, *69*(2), 200-213.

Hockett, C. F. (1961). Linguistic elements and their relations. *Language*, *37*, 29-53.

Hrvoj-Mihic, B., Bienvenu, T., Stefanacci, L., Muotri, A. R., & Semendeferi, K. (2013). Evolution, development, and plasticity of the human brain: from molecules to bones. *Frontiers in Human Neuroscience*, *7*, 707.

Hurford, J. R. (2003). The language mosaic and its evolution. In M. Christiansen & S. Kirby (Eds.), *Language Evolution* (pp. 38–57). Oxford University Press.

Izhikevich, E. M., & Edelman, G. M. (2008). Large-scale model of mammalian thalamocortical systems. *Proceedings of the National Academy of Sciences*, *105*(9), 3593-3598.

Jackendoff, R. (2003). Précis of foundations of language: brain, meaning, grammar, evolution. *Behavioral and Brain Sciences*, *26*(6), 651-665.

Juarrero, A. (1999). *Dynamics in action: Intentional behavior as a complex system*. Cambridge, MA: MIT press.

Kello, C. T. (2013). Critical branching neural networks. *Psychological Review*, *120*(1), 230-254.

Kelso, J. A. S. (1995). *Dynamic patterns: The self-organization of brain and behavior*. Cambridge, MA: MIT Press.

Kelso, J. S., Tuller, B., Vatikiotis-Bateson, E., & Fowler, C. A. (1984). Functionally specific articulatory cooperation following jaw perturbations during speech: evidence for coordinative structures. *Journal of Experimental Psychology: Human Perception and Performance*, *10*(6), 812.

Knobe, J. (2003). Intentional action and side effects in ordinary language. *Analysis*, *63*(279), 190-194.

Lashley, K.S. (1951). The problem of serial order in behavior. In L.A. Jeffress (Ed.), *Cerebral mechanisms in behavior* (pp. 112-135). New York: Wiley.

Louwerse, M. M., Dale, R., Bard, E. G., & Jeuniaux, P. (2012). Behavior matching in multimodal communication is synchronized. *Cognitive Science*, *36*(8), 1404-1426.

Maass, W., Natschlager, T., & Markram, H. (2002). Real-Time Computing Without Stable States: A New Framework for Neural Computation Based on Perturbations. *Neural Computation*, *14*(11), 2531-2560.

MacWhinney, B. (1999). *The emergence of language*. Lawrence Erlbaum.

Mantini, D., Corbetta, M., Romani, G. L., Orban, G. A., & Vanduffel, W. (2013). Evolutionarily novel functional networks in the human brain? *The Journal of Neuroscience*, *33*(8), 3259–3275.

Mitchell, M. (2009). *Complexity: A guided tour*. Oxford University Press.

Moretti, P., & Muñoz, M. A. (2013). Griffiths phases and the stretching of criticality in brain networks. *Nature Communications*, *4*, 2521.

Nieuwenhuys, R. (1994). The neocortex. *Anatomy and Embryology*, *190*(4), 307–37.

Oller, D. K. (2004). Underpinnings for a theory of communicative evolution. In D. K. Oller & U. Griebel (Eds.) *The Evolution of Communication Systems: A Comparative Approach* (pp. 49-65). Cambridge, MA: MIT Press.

Ramchand, G., & Reiss, C. (2007). *The Oxford handbook of linguistic interfaces*. Oxford University Press.

Riley, M. A., Richardson, M. J., Shockley, K., & Ramenzoni, V. C. (2011). Interpersonal synergies. *Frontiers in Psychology*, *2*.

Ringo, J. L. (1991). Neuronal interconnection as a function of brain size. *Brain, Behavior and Evolution*, *38*(1), 1-6.

Schoenemann, P. T. (1999). Syntax as an emergent characteristic of the evolution of semantic complexity. *Minds and Machines*, *9*(3), 309–346.

Schoenemann, P. T.. (2006). Evolution of the Size and Functional Areas of the Human Brain. Annual *Review of Anthropology*, *35*, 379–406.

Schoenemann, P. T. (2009). Evolution of brain and language. *Language Learning*, *59*(Supplement 1), 162–186.

Schoenemann, P. T. (2012). Evolution of brain and language. In M. A. Hofman & D. Falk (Eds.), *Progress in Brain Research* (Vol. 195, pp. 443–459). Amsterdam: The Netherlands: Elsevier.

Seidenberg, M. S., & MacDonald, M. C. (1999). A probabilistic constraints approach to language acquisition and processing. *Cognitive Science*, *23*(4), 569–588.

Syal, S., & Finlay, B. L. (2011). Thinking outside the cortex: social motivation in the evolution and development of language. *Developmental Science*, *14*(2), 417-430.

Tononi, G., & Edelman, G. M. (1998). Consciousness and complexity. *Science*, *282*(5395), 1846–1851.

Van Den Berg, C. (2000). A dynamical systems approach to movement coordination. *Netherlands Journal of Zoology*, *50*(2), 163-178.

von Holst, E. (1939/73). The behavioral physiology of man and animals. In R. Martin (Ed.), *The Collected Papers von Holst*. Coral Gables, FL: University of Miami.

Van Orden, G., Hollis, G., & Wallot, S. (2012). The blue-collar brain. *Frontiers in Physiology*, *3*.

Watumull, J., Hauser, M. D., Roberts, I. G., & Hornstein, N. (2013). On recursion. *Frontiers in Psychology*, 4, 1017.

Workman, A. D., Charvet, C. J., Clancy, B., Darlington, R. B., & Finlay, B. L. (2013). Modeling transformations of neurodevelopmental sequences across mammalian species. *The Journal of Neuroscience*, *33*(17), 7368-7383.