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<RH>*Commentary/Anderson: Précis of After Phrenology: Neural Reuse and the Interactive Brain*

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<CT>**Why a developmental perspective is critical for understanding human cognition**

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<C-AB>**Abstract:** The evidence that Anderson (2014) marshals in support of his theory of neural reuse is persuasive. However, his theoretical framework currently lacks a developmental dimension. We argue that an account of the fundamental aspects of *developmental change*, as well as the *temporal context* within which change occurs, would greatly enhance Anderson's theory.

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A number of theories have been put forward with the aim of unifying and providing a framework for the neural and psychological sciences. Do we need another one? According to Anderson (2014), yes, we do. Anderson argues that many current theories are based on suppositions that are demonstrably false, such as the assumption that the mind is modular (Barkow et al. 1992; Sternberg 2011) or that neurons and neuronal populations reach a state in which they can respond only to a specific and restricted set of stimuli (Johnson 2001; 2011). On the contrary, according to Anderson, the brain is a continuously self-organising system; neurons are adaptively recruited in real time into partnerships to form hierarchies at multiple levels and timescales, but these partnerships are never truly *fixed* (“neural reuse”).

We agree with Anderson’s view that neural circuits can be put to multiple uses. His theory of neural reuse can indeed explain a range of phenomena, from synaesthesia to cross-modal plasticity (where a cortical area for one function [e.g., vision] is used for a different one [e.g., hearing in blind persons]). However, although Anderson’s framework was motivated “first and foremost by functional, *developmental*, and evolutionary considerations” (p. 95, italics added), he actually focuses on activity at multiple *physical* – but not temporal – scales. Yet, understanding developmental processes – at multiple timescales – is crucial to understanding brain function. Therefore, we believe that an account of the fundamental aspects of developmental change, as well as the *temporal context* within which change occurs, would greatly enhance Anderson’s theory.

The reason an emphasis on *development* is critical for understanding brain function is that (embodied, social) brains are adaptive “complex” systems, and complex systems are *history*

dependent (Buzsaki 2006; Kelso 1995). In other words, the brain does not comprise neural and cognitive modules that passively process sensory information in order to prepare a behavioural response. Rather, much of the brain's activity is self-generated; sensory inputs help the brain to adjust its "internal connectivity and computations to the spatial and temporal metrics of the external world" (Buzsaki 2006, p. 11). That is, sensory information "gets embedded into a context, an important part of which is time" (Buzsaki 2006, p. 11). For example, auditory perception depends both on the perceiver's brain state and past experience with physical inputs, as well as on the pattern of sound vibrations reaching the cochlea. Hence, as Buzsaki (2006) argues, "each time the same stimulus is presented, it generates a somewhat different and unique trajectory in the neuronal space" (p. 13).

Anderson alludes to the importance of the temporal dimension throughout his book, but rarely does he actually take time into account. For example, how might neural reuse explain the finding that, after brain insult, recovery of function is massively dependent on *time*-related variables such as *age* at insult (e.g., Anderson et al. 2010)? Yet, such a discussion might actually strengthen Anderson's theory. For instance, it is widely assumed that early insults are distinct from those occurring in adulthood, and consequently that the infant brain is more plastic than the adult one. For example, whereas children with perinatal left-hemisphere (LH) damage acquire age-appropriate language skills, adults with similar LH lesions typically present with aphasia (Bates et al. 2001; Ricci et al. 2008). According to Johnson's (2001; 2011) Interactive Specialization framework (and the broader neuroconstructivist approach; Elman et al. 1996; Mareschal et al. 2007), this reduction in plasticity is a consequence of neural commitment, because functional brain development is characterised by a process of increased tuning or

selectivity of functions (see discussion in Thomas 2003). However, recent evidence has yielded a more complex, nonlinear relationship between (for example) age of insult and recovery (Anderson et al. 2010; see Anderson et al. 2011, for review). For example, Vicki Anderson and colleagues (2010) found that children who had sustained brain injury prior to 2 years of age performed *worse* on a range of standardised neurobehavioural measures than those who had acquired brain insults after 7 years of age, indicating “greater early vulnerability” rather than “greater early plasticity”. How can our current theories explain such findings? Could the early brain insults have had cascading effects on the developing system? Could the fact that plasticity occurs on different timescales – from spine plasticity (minutes) to the reorganization of large functional networks (days, months) – help explain differences in recovery outcome? Indeed, a review by Vicki Anderson et al. (2011) suggests that neither plasticity nor vulnerability theories explain the wide range of functional outcomes after brain insult (see also Giza & Prins 2006; Mosch et al. 2005). On the contrary, many different (time-related) developmental and environmental factors are involved (Anderson et al. 2011). A theory that takes development seriously (e.g., dynamic systems theory, neuroconstructivism) may have greater success in explaining these time-related phenomena.

Timing is also important in understanding the *typically developing* (TD) brain. Take learning, for example. The acquisition of new skills over the lifespan is constrained by *age* of acquisition; early learning constrains the development of later cognitive and neural structures (Hernandez & Li 2007). For example, in the language domain, young children gain much deeper grammatical sensitivity when learning new languages than (cognitively superior, even fluent-speaking) adults (Johnson & Newport 1989). Why do we not learn equally well over the

lifespan? How does neural reuse help explain, for example, why adult Japanese speakers who learn English as a second language often have great difficulty in discriminating /r/ from /l/ accurately? Takagi and Mann (1995) examined the perception of /r/ and /l/ in adult Japanese learners of English as a function of their exposure to the English language. They found that although persistent exposure (12 or more years in an English-speaking environment) improved /r/-/l/ identification accuracy, the learners never attained perfect perceptual mastery (see also Flege et al 1999; Takagi 2002; for reviews, see Birdsong 2006; Hernandez & Li 2007). Yet, infants worldwide can initially perceive all the phonetic and phonemic differences across languages (e.g., whatever their mother tongue, early on all can discriminate between English /r/ and /l/) and have the potential to master multiple languages (Eimas 1975). Nevertheless, infants' perception of *nonnative* distinctions declines during the second half of the first year of life (Werker & Tees 1984), and their ability to discriminate *native* speech sounds increases (Kuhl et al. 2006). This developmental process (known as *perceptual narrowing*) is clearly important, because it correlates with greater language and reading skills later in life (Kuhl et al. 2008). But it also suggests that the neural commitment arising from learning a language early in development decreases the ability to learn other languages later on in development (Kuhl 2004).

Neuroconstructivism can explain perceptual narrowing, because accounts of perceptual narrowing involve “neural commitment” (Kuhl 2004) or “restriction-of-fate” (Mareschal et al. 2007), whereby the neurocognitive functions involved in human perception gradually “specialize” over developmental time for socially relevant information – in faces, voices, music, language, and action (e.g., Lewkowicz & Ghazanfar 2009; Scott et al. 2007; Werker & Tees 2005; see Pascalis et al. 2014, for discussion). Anderson's framework can also account for these

developmental data, by arguing that the early formation of functional networks constrains the emergence of future ones. Moreover, there is evidence that perceptual narrowing can be reversed in 9-month-old infants under certain conditions (Kuhl et al. 2003), which fits well with the concept of neural reuse. But a focus on developmental change of this nature is missing from Anderson's book. Precisely *what* is the difference between infants and adults in these kinds of studies? *Why* are neurons or neuronal populations not being reused to help Japanese adult learners of English (i.e., perceptual narrowing has not been reversed in children older than 9 months)? *How* are later emerging networks constrained by the existence of earlier developing ones?

Developmental change is also crucial for understanding *individual differences*. As Anderson acknowledges, the emergent behaviour of a system (e.g., social anxiety in an individual) is not reducible to the microstates of the system's parts (e.g., genes, neurons). Rather, emergent properties arise as a result of additional laws that apply at higher levels. These additional laws, which include *developmental* principles, as well as principles of functional brain organisation and social context, constrain the arrangement and behaviour of the components at levels below, and help to explain why particular properties (e.g., social anxiety) are present in some individuals but not in others. Moreover, because complex systems tend to gravitate towards certain stable patterns of activity (Kitano 2004; Thelen & Smith 2006), understanding developmental processes can also help to explain why qualitatively new and unexpected functional states emerge (e.g., psychosis). Furthermore, it can help explain why some states (e.g., psychosis) are relatively common. Some states can induce changes in the system that make it more likely for them to re-emerge in the future. For example, there is evidence that normal

homeostatic processes in dopaminergic signalling pathways can, under certain circumstances, compound the effects of perinatal deficits in the brain – and subsequently drive the system into psychosis and (thereafter) schizophrenia (e.g., Lisman et al. 2008). Hence, brain structure and function are deeply yoked to developmental processes, and therefore we must consider developmental trajectories when striving to account for individual differences and especially when trying to understand how various neurodevelopmental disorders arise (Karmiloff-Smith 1998). This is especially important if, as Anderson contends, relations between neurons (or populations of neurons) are never fixed but vary over time.

Therefore, thinking *developmentally* can help the scientist to understand a range of phenomena that are related to brain structure and function. Important developmental questions include: Is there more neural search early on in life? How and when ontogenetically does neural reuse actually occur? Some groups of neurons (e.g., those in anterior insula) are more functionally diverse than others (e.g., those in primary visual cortex) (Anderson 2014): Do all groups of neurons start off functionally diverse, with some becoming more specialised than others over developmental time? Do the (low-level) functional biases of local networks also change over time? As coalitions of neurons emerge and grow in strength, does the brain become progressively less plastic? If neurons used for processing objects become co-opted into learning a language, does that affect their role in object processing? Or can neurons be “reused” without any cost (see Liu et al. 2015, for evidence of neural trade-offs)? Does the brain develop from a relatively labile state to one that falls in between labile and stable, or is it always labile? The neural reuse theory accounts for rapid online adaptivity to changing environments. But is this plasticity unconstrained – i.e., might it produce a brain that is *too* malleable (Bavelier et al. 2010;

Hensch 2005; Karmiloff-Smith 2015)? If neurons can be co-opted into different coalitions without any cost, then how would neural reuse explain phenomena such as the developmental “rise and fall” of synaptic density (Goddings & Giedd 2014; Huttenlocher 1990; 1994), “U-shaped” curves in development (e.g., Casey et al. 2010; Giedd & Rapoport 2010; see Rogers et al. 2004, for discussion), or perceptual narrowing in infants (Werker & Tees 1984)? The preceding are all fundamentally developmental questions. A developmental perspective is, in fact, crucial because the *timing* of developmental events is likely to be an important constraining factor.

In conclusion, Anderson’s idea that neurons are recruited into partnerships that are never fixed is a compelling one. However, we argue that at every level of an adaptive, complex system, one cannot ignore its developmental history and environmental context. Hence, an understanding of the human mind/brain requires a truly developmental perspective that, in our view, would greatly enhance Anderson’s theoretical framework.

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