Contemplating the GANE model using an extreme case paradigm

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ABSTRACT (ENGLISH)

Early experiences play a crucial role in programming brain function, affecting selective attention, learning, and memory. Infancy literature suggests an extension of the GANE (glutamate amplifies noradrenergic effects) model to conditions with minimal priority-map inputs, yet suggests qualifications by noting that its efficacy is increased when tonic levels of arousal are maintained in an optimal range, in manners that are age and exposure dependent.

FULL TEXT

Mather and colleagues' intriguing GANE (glutamate amplifies noradrenergic effects) model underscores an important process, through which GANE changes influence the selection process to favor high- over low-priority representations.

The extended literature covered in the article concentrates mostly on experimental research with typically developing young adults, whose performance relies on an established neural network, set with implicit “know-hows” and an explicit knowledge base, which shape and set local hotspots, to be activated proactively in the prospect of newly arriving inputs (Bouret &Richmond 2015). One way to test this model may be an extreme case paradigm in which top-down priorities are negligible, and the roles of global brain activation are augmented, as is the case of the newborn.

Research on infancy, early development of attention, and arousal, in typical and clinical samples opens the discussion of the generalizability of the GANE model because young infants perceive stimuli with no preset priorities and with little previous knowledge. As such, infancy offers an interesting test case for the GANE model.

Early-life experiences play a crucial role in programming brain function, particularly with respect to selective attention, learning, and memory (Geva et al. 2006). Newborns are busy perceiving and memorizing the environment at rates that are not surpassed thereafter, equipped with an impressionable template that does not allow yet for exerting deliberate priority operations. How might GANE function at infancy?

Models with neonates highlight four interdependent notions that may qualify the limits of the proposed model, with respect to development, exposure, global activity, and resilience to variance.

Dependence on development

Neonates and adults differ markedly in their ability to learn selectively (Kuhl et al. 1992). These differences were suggested to be related, in part, to developmental differences in arousal response to sensory stimuli (Kuhl 2007) as a function of differential locus coeruleus–norepinephrine (LC–NE) activity (Moriceau &Sullivan 2004; Nakamura &Sakaguchi 1990). Differences are such that compared with the LC of the infant, the adult LC gradually becomes less likely to respond to non-noxious stimuli (Kimura &Nakamura 1985; Nakamura et al. 1987; Selden et al. 1990), habituates earlier in response to repeated (or even single) stimulation (Vankov et al. 1995), and produces shortened LC responses in response to sensory stimulation (Nakamura &Sakaguchi 1990). All of these differences suggest a potential role for development in the proposed model (Moriceau &Sullivan 2004).

Dependence on experience

Exposure at sensitive periods seems to play a significant role in the development of the LC–NE system (Nakamura et al. 1987; Rangel &Leon 1995). Also, experience early in development has been found to affect PFC responsivity to LC–NE. For example, neonatal experience involving maternal contact reward was reported to affect the noradrenergic system of the rat prefrontal cortex (Kalpachidou et al. 2015). The experience was related to hypomethylation of the β_1-adrenergic receptor gene promoter and consequently enhanced expression of its mRNA in the prefrontal cortex, resulting in better discrimination and improved learning in the young pups (Kalpachidou et al. 2015).

In addition, selective recognition of maternal odors has been found to be accompanied by increased release of glutamate and GABA from the dendrodendritic synapses and an increased efficacy of glutamate-evoked GABA release (Kendrick et al. 1992), and early-life stress related to maternal separation has been reported to alter glutamate and GABA transmission and, in particular, to alter $GABA_A$ receptor expression (Sterley et al. 2013). The integration of these findings points to the possible role of early-life exposure in the GANE model.

Dependence on tonic levels of activity

The LC is thought to play a central role in regulating arousal states in addition to its role in attention and memory (Howells et al. 2010; Rajkowski et al. 1994). Initial leads from human infancy research point to the notion that in the case of the newborn, arousal homeostasis possibly plays a significant role in attention and in recognition (Geva et al. 1999), with brainstem pathways playing a central role in gating arousal self-regulation (Geva &Feldman 2008). Feeding-dependent arousal differences were found to affect newborn preferences for cognitively demanding stimuli (Geva et al. 1999; 2013), the interaction is such that more aroused neonates tend to orient toward less intense familiar stimuli; yet when less aroused, newborns prefer more intense stimuli (Gardner &Karmel 1983; 1984) and orient toward novel stimuli as compared with familiar ones in visual recognition memory tasks (Geva et al. 1999). Sleep–wake arousal states also seem to play a similar role. Recent work with intracellular recordings has shown an interaction of LC activity in monkeys as a function of fatigue, an effect attributed to the LC possibly providing the impetus to act when the predicted outcome value is low (Bouret &Richmond 2015). Indeed, arousal states were found to affect attention in young human infants. Neonatal sleep fragmentation was reported to be associated with infants' focused attention to specific stimuli early in development (Geva et al. 2013). Compared with good sleepers, infants who were poor sleepers as neonates had difficulties focusing on target stimuli in the presence of complex distracters, but managed focusing in the presence of simpler distracters. Integration of the findings on arousal state effects on attention and memory emphasizes the need to consider tonic arousal changes in the GANE model.

Finally, the validity of the model may gain from testing of its limits in neuropsychiatric disorders, such as attention-deficit/hyperactivity disorder (Sterley et al. 2013), which involve poor adaptation to change (Sara 2009). Such an exploration may suggest the notion that GANE efficacy is increased when tonic levels of arousal are maintained in an optimal range.

Together, these data suggest an extension of the GANE model to infancy; however, integration of the above findings with the framework presented suggests a qualification to the GANE model, by noting that its efficacy is increased when tonic levels of arousal are maintained in an optimal range, in manners that are age and exposure dependent.

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