



Review

Promoting our understanding of neural plasticity by exploring developmental plasticity in early and adult life



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ABSTRACT

Developmental plasticity (DP) is widely considered to be a property of early life stages, but evidence suggests it can be reactivated in mature brains. For example, recent developments on animal models suggest that experience in enriched environments (EE) can induce DP and enable adult recovery from amblyopia; even when the typical critical period for that recovery has closed. An interesting body of evidence suggests that extrapolation of the rejuvenatory power of that paradigm in mature human brains is feasible. These studies show that exposure to EE throughout life is associated with a delay, or even prevention, of age-related cognitive deficits. Consequently, it can be concluded that DP might underlie the neuroprotective effects against a neurocognitive breakdown that have been observed, and that EE exposure later in life might induce DP in a similar way to early EE exposure. Thus, the DP might exert its influence beyond the typical developing age ranges: childhood and adolescence. Although further research is still required, the observation of EE related neuroprotective effects are a breakthrough in the study of DP in humans and new advances in our understanding of neural plasticity have thus been reached.

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1. Introduction

The discovery by the Nobel Prize winning scientists Hubel and Wiesel of a critical period in early postnatal life for treating strabismus in cats (Hubel and Wiesel, 1970) stimulated further efforts in the study of the role of experience in the development of visual perception and the sensory systems. Consequently, the existence

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of sensitive, or critical, periods in early postnatal life has been rigorously documented: thus reinforcing the special prominence of DP in brain maturation. DP refers to changes in neural connections that occur during development and which are induced by learning or environmental interactions. Sensitive/critical periods can be defined as developmental phases during which there is a biological display of an extreme neural sensitivity to the storage of experience-driven information. Sensitive periods thus safeguard a normal development of sensory systems and promote an individualized design of the shape and function of the neural circuits, which contribute to the individual's survival (Hensch, 2004; Spolidoro et al., 2009).

On the other hand, several papers have been published that have used a variety of methods to examine the restoration of DP: synaptic plasticity, within the adult visual system of animals (e.g. Pizzorusso et al., 2002; McGee et al., 2005; Pizzorusso et al., 2006; He et al., 2006, 2007). Interestingly, Sale et al. (2007) observed a reactivated juvenile-like plasticity in adult amblyopic rats after their exposure to an EE. An EE is characterised by its stimulant complexity (Rosenzweig, 1966; Walsh, 1981; Rosenzweig, 2003; Pinaud, 2004), which may include higher than normal frequency or duration of social contacts, numbers of novel objects, and/or numbers of opportunities for engaging in physical exercise (Lewis, 2004; Will et al., 2004) within the individual's surrounding context.

Moreover, the authors discovered that this rearing environment reduced the molecular mechanism that had previously been proposed to be involved in reducing DP over the course of brain maturation: the intra-cortical inhibition mechanism.

In this contribution, I begin with a discussion of the most representative evidence of the early impact of DP on the brain and on cognition. My focus then concerns the relatively new insights that point to a reactivation of DP in the animal adult visual system; with a special emphasis on the advantageous DP-inductor role of EE. The discussion will then address the scientific literature on the effects of EE exposure in humans in terms of potential parallels with reactivated DP in adult animal life. Taken together, the evidence reviewed here suggests a continued impact of the DP on brain and cognition until well into adulthood rather than an action of DP that is strictly restricted to early life-stages. This conclusion is supported by the discussion of the results of several neuroimaging studies, which also point to this extended DP-related influence. Finally, a short reflection on the evolution of our understanding of neural plasticity is presented as the basis for proposed future research work.

2. Evidences of sensitive/critical periods (DP) in early postnatal human life

There are multiple sensitive/critical periods for different aspects of, and within, each sensory modality (e.g. Johnson, 2005). For example, it has been consistently demonstrated within the visual domain that an imbalance in binocular vision due to monocular deprivation during childhood affects visual acuity in humans and causes amblyopia in the affected eye (Medini and Pizzorusso, 2008). If a child does not undergo surgery to rectify this condition prior to puberty, the risk of losing the eye increases significantly (Morales et al., 2003). Lewis and Maurer (2005) conducted a longitudinal behavioural study and found different sensitive/critical periods; between six and 14 years of age, for normal development, damage induction, and damage recovery of different aspects of vision, such as visual acuity and peripheral vision. The development of the human auditory system is also affected by experience during sensitive/critical periods in at least three ways. Firstly, early auditory experience shapes auditory function; especially with regard to the speech perception that is inherent in humans. Kuhl (2004) concluded that neonates are able to distinguish among

phonemes of different languages during the first year of life; with this ability diminishing with increasing age. Secondly, early auditory deprivation produces an abnormal subsequent development of auditory function, when compared with that of normal hearing subjects (Sininger et al., 1999). Finally, early intervention by means of cochlear implantation favours the rehabilitation of auditory alterations (Morales et al., 2003). The critical period for that rehabilitation may be between the ages of four to six years (Harrison et al., 2006; Kral et al., 2006; Giraud and Lee, 2007), with a reduced likelihood of a full recovery if the cochlear intervention is applied after age of seven (Sharma et al., 2005).

There is also evidence of a long-lasting impact of early learning experiences on lower-order processing, such as the acquisition of gustatory and olfactory preferences. Within the gustatory domain, high correlations have been reported (see Trubulsi and Mennella, 2012) between the food preferences acquired during early infancy: two to three years of age, and the status of such preferences in late childhood (Skinner et al., 2002), adolescence (Nu et al., 1996) and young adulthood (Nicklaus et al., 2004). In the case of olfactory preferences, the available evidence points to the perinatal time as a sensitive/critical period for postnatal olfactory learning. Romantshik et al. (2007) found that perinatal exposure of full-term neonates to specific odours correlated with preference for those odours, over other odours, at later stages of development.

Furthermore, several kinds of learning that imply both higher-order and lower-order processing, also suggest the critical role of experience during sensitive/critical periods; with this experience inducing a facilitator effect. The human-specific capacity of acquiring verbal language is a commonly cited example (Nordeen and Nordeen, 2004; Thomas and Johnson, 2008; Thomas and Knowland, 2009; Howard-Jones et al., 2012). The age of two appears to be a critical period for the acquisition of a child's native language while the age of four appears critical for the acquisition of a second language with native expertise (Giraud and Lee, 2007). Emerging research also points to the existence of sensitive/critical periods for musical learning (see Trainor, 2005 and Penhune, 2011 for reviews).

We can conclude that the effects of experience during postnatal sensitive/critical periods are linked to the acquisition of essential abilities that enable individuals' management of daily situations with sufficient efficacy; with these abilities providing subjects with the capacity for appropriate behavioural responses according to a given circumstance. However, these effects are not always innocuous. For example, research that has been carried out on the human limbic system shows that early maternal or social deprivation, or any other kind of maltreatment or abuse, produces persistent damage (Joseph, 1999; McCollum, 2006). The main consequences include a long-lasting irritability of this neural system: even in the adult life, which is manifested in a behavioural hypersensitivity to stress (Teicher, 2002; Andersen and Teicher, 2008), and a constant state of alarm that leads to the individual scanning the environment in search of imminent dangers (Pruessner et al., 2009). DP ensures the adequate development of the nervous system by shaping neural circuits according to the individual's environment-related experience; thus enhancing the chances of survival within that unique context.

3. Evidences of induced DP in mature life via EE

3.1. EE

EE are rearing conditions that evolved into a classical experimental paradigm in the field of neural plasticity in the 1960s and 70s. Rosenzweig's and Greenough's groups began to systematically explore plastic effects of this rearing condition on animal brains; in particular on their cognitive functional development (e.g. Krech

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