Brain plasticity and education

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Abstract. Functional plasticity is the ability to change behaviour based on experience. In education, that experience is typically derived from structured learning environments. It is widely held that functional plasticity changes with age, reducing after mid-childhood, and that structural changes in the brain are responsible for this reduction. The implication is that after mid-childhood, it is harder for individuals to learn. In this article, we review research from neuroscience and from psychology to address three questions relevant for education: (1) Why does functional plasticity reduce? (2) When does functional plasticity reduce? And, (3) How can learning be best achieved when functional plasticity has reduced? The main conclusion is that while, on the whole, plasticity does reduce with age, the rate is different across different abilities (and components of abilities) and there are no sudden cut-offs, with some degree of plasticity usually remaining. Higher cognitive abilities appear to have more extended plasticity than sensory or motor skills. Finally, we review recent evidence on individual differences in plasticity, and research investigating techniques for enhancing brain plasticity.

Introduction

In this article, we consider how findings on brain plasticity inform education. In particular, we consider the implications for learning of changes in brain plasticity with age. There is a widespread and broadly correct view that functional plasticity – the ability to change behaviour based on experience – reduces after mid-childhood, and that structural changes in the brain are responsible for this reduction. One might therefore conclude that an educational curriculum would be optimised if the age at which each academic subject or skill is taught coincided with the maximum plasticity of the brain systems involved (Thomas & Knowland, 2009). Sometimes, the idea that plasticity reduces with age is used to draw more extreme conclusions, for example, that children should be taught as much as possible as early as possible to maximise educational outcomes.

Before we review the neuroscience behind these views, it is worth making two points. First, an understanding of brain plasticity does not directly or uniquely constrain decisions about education. For example, as we will see, there is little current evidence that the brain's plasticity for

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learning to read reduces with age. The decision about when children should be taught to read, whether it is 5 or 7 or 9 (or earlier or later), must therefore be guided by other factors. One could argue that exposing children to formal instructional situations at an early age is counter-productive, when their mode of learning should be via spontaneous exploration. Or one could argue that the earlier a child learns to read, the sooner the child will gain access to the vast store of knowledge available through books. The point is that in this case, the data from neuroscience are neutral. Secondly, successful learning in the classroom does not solely rely on the brain's plasticity. Learning within an educational setting relies on children possessing a wider skill set, including the ability to follow directions, the ability to communicate wants, needs and thoughts verbally, the ability to be enthusiastic and curious in learning and the ability to be sensitive to the feelings of other children (Blair & Diamond, 2008). (One could, of course, argue that these skills are the result of brain plasticity operating at an earlier stage in life). Moreover, in parallel with cognitive abilities, there are age-related changes in physical, emotional, social and sexual development, and an increasing importance of the peer group on individual learning, each of which may influence educational success. In what follows, we focus on brain plasticity alone, but findings from neuroscience constitute just one constraint to inform decisions on education.

Why does plasticity reduce with age?

Functional plasticity is the idea that experience can change behaviour. Changes in behaviour are produced by changes in the underlying brain mechanisms, and structural plasticity refers to the flexibility of these underlying mechanisms to generate changes in behaviour. The reason for distinguishing between functional and structural plasticity is that functional plasticity refers solely to observed rates of change in behaviour. Behavioural changes may be realised by multiple different underlying mechanisms, so that structural plasticity may related to functional plasticity in multiple ways. The idea that plasticity reduces with age has a long history, first becoming known with the phenomenon of filial imprinting described by Konrad Lorenz (see Johnson, 2005, for a review). After a relatively brief exposure to a particular stimulus early in life, many birds and mammals form a strong and exclusive attachment to that stimulus. The idea of a *critical period* for learning is that plasticity is confined to a short and sharply defined period of the individual's life, and that later experience cannot reverse this experience. Subsequent research with a range of species demonstrated that such periods of heightened plasticity are a major phenomena in behavioural and brain development, but that periods of plasticity do not end so abruptly and are not as irreversible as first thought (Bolhuis, 1991; Michel & Tyler, 2005; Thomas & Johnson, 2008). The term *sensitive period* was therefore preferred. From an educational perspective, it is worth noting that the concept of sensitive periods predominantly arises from work on perception, not higher cognition (i.e., skills such areas as literacy, numeracy, and reasoning).

Johnson (2005) identified three classes of explanation for the end of sensitive periods, that is, for why functional plasticity should reduce. The first class is that the termination arises from internal factors controlled by maturation or an external environmental trigger. The second class is that learning is self-terminating, in that the system drives itself into a representational state where it is no longer responsive. The third class is that underlying plasticity does not actually reduce but the constraints on plasticity (such as environmental inputs) become stable. The three are not mutually exclusive, and each may account for sensitive periods in different skills. A key dimension in this (continuing) debate is whether specific mechanisms underlie sensitive periods or whether such periods are a natural consequence of functional brain development (see Thomas & Johnson, 2008, for discussion). For example, in Johnson's (2001) *interactive specialisation* theory, functional brain development in cerebral cortex involves a process of increasing specialisation

of response properties. Some cortical regions begin with poorly defined response functions and are engaged by a range of different contexts and tasks. During development, competitive activity-dependent interactions between regions fine-tune their functions. A brain region's activity becomes restricted to a narrower set of stimuli or task demands. Under this view, plasticity reduces as a natural consequence of this developmental process: once regions have become specialised for their adult functions, these commitments become difficult to reverse (Johnson, 2005).

Research using neurocomputational models of development has indicated that several mechanisms can in fact serve to reduce the functional plasticity of a learning system (Thomas & Johnson, 2006). These can be classified according to Johnson's scheme. Under *internal factors*: there may be loss of computational resources over time, so there is less capacity to acquire new skills – poorer capacity is associated with poorer learning. Or there may be a change in the mechanisms that modulate the strength in connectivity between neurons or the response dynamics of neurons (see Bavelier, Levi, Li, Dan, & Hensch, 2010). Under *self-terminating*: there may be competition for computational resources, whereby an earlier acquired skill takes control of neural resources and a later skill must compete for these resources in order to be learned. Or there may be entrenchment, in which during an earlier phase of learning, a computational system has adopted a state that is sub-optimal for learning a new skill. Learning the new skill will take additional time simply because the earlier state must be undone, even if intrinsic structural plasticity itself has not reduced. Under *stabilisation*: A more subtle loss of plasticity can be caused by a process of assimilation. The formation of stable representations of one set of information stops the system from perceiving new, different information because that information is simply assimilated via top-down processes into old information. If the system cannot perceive changes in the world, it cannot adapt to them. In this case, even though the system has not lost intrinsic plasticity, it will appear to have done so because it cannot detect the changes to which it should respond.

An understanding of mechanism highlights the point that reductions in functional plasticity can be explained by multiple changes in structural properties. Depending on which mechanism is responsible, plasticity may be restored by different methods. For example, if competition is the cause, cease the competing behaviour while acquiring the new behaviour. If resource loss is the cause, increase the level of practice and/or focus on regular, systematic domains of knowledge which are more easily acquired with limited resources. If assimilation is the cause, use exaggerated exemplars of the new information, which makes this information appear more different from the old knowledge and therefore less prone to be assimilated into old knowledge.

To date, much research within psychology and education has focused on identifying what skills can be acquired at different ages (see next section), and we are still at an early stage in identifying which mechanisms may be responsible for which age-related differences. We know that many of the above manipulations can increase functional plasticity for particular behaviours (Thomas & Johnson, 2008). For example, assimilation is held to be one reason why it is hard to distinguish phonemic contrasts in non-native languages, and it has been demonstrated that the use of exaggerated exemplars of these phonemes helps adults to learn such contrasts (McCandliss, Fiez, Protopapas, Conway, & McClelland, 2002).

We also know that the brain exhibits marked structural changes with age, including the loss of neurons and the pruning of connections. MRI data is one method to reveal age-related changes. Figure 1 illustrates two functions, one linking global grey matter volume with age and the other linking global white matter volume with age, from 7 to 73 years, for a sample of around 80 individuals (Richardson, Thomas, Filippi, Harth, & Price, 2010). Grey matter consists of neuronal cell bodies, local connectivity, nerve fibres, capillaries and glial cells, while white matter reflects the connecting fibre pathways (Stiles, 2008). Figure 1 shows that grey matter declines across the age range considered. White matter, however, increases right up until 50 years of age, and then can show a small decline associated with ageing. Direct links between

these global measures of brain structure and behaviour are not straightforward. One simplistic view is that the decline in grey matter indexes a loss of processing resources, while the increase in white matter indexes the increase in established knowledge. If this view is correct, some reductions in functional plasticity are likely to arise from changes in intrinsic brain properties, since we saw that on computational grounds, reduced resources are one mechanism that can lead to a reduction in functional plasticity. However, as we shall see, there is evidence that changes in brain structure with age are not uniform across the brain but are non-linear and region specific.

Lastly, an understanding of the mechanism explaining the relationship between functional plasticity and age is rendered more complex by a range of confounding factors correlated with increases in age. For example, adults who acquire skills later in life may have less time to practise those skills; adults may be less motivated to acquire new behaviours than children; adults may be able to complete novel tasks by employing their existing abilities in strategic ways without having to acquire new skills. Although there has been progress in understanding the mechanisms underlying plasticity, there is still much to do in unpicking the factors that influence changes in functional plasticity with age. We now turn to consider when plasticity appears to be at its maximum for acquiring different behaviours.
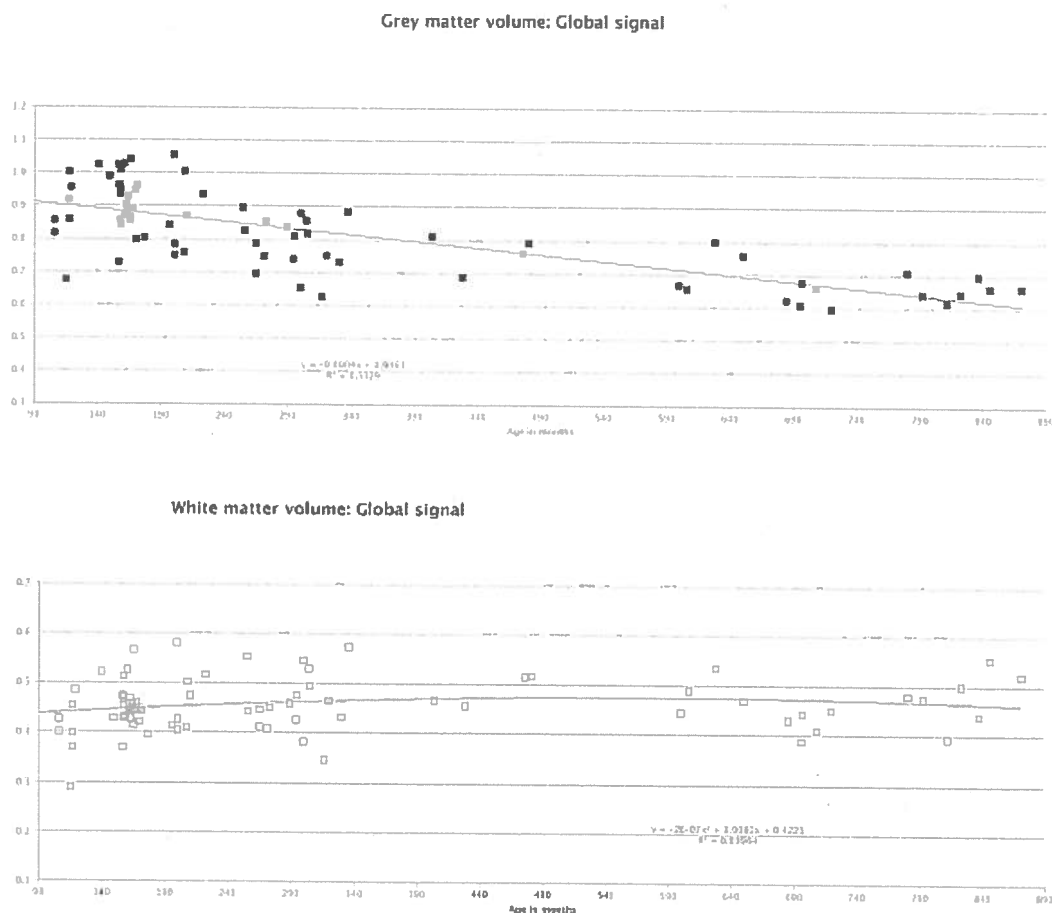

Figure 1. Global grey matter and white matter signals for a sample of 77 individuals between the ages of 7 years and 5 months and 72 years and 7 months (Richardson, Thomas, Filippi, Harth & Price, 2010). Data show modulated images of grey and white matter volume.

At what age does plasticity reduce?

To ask this question is to assume that the relationship between functional plasticity and age is *non-linear*; that is to say, at some age, a decline in plasticity begins, or the rate of decrease becomes faster. A number of functions have been proposed for how plasticity may change with age (Birdsong, 2005). Figure 2 depicts three of these functions. Figure 2(a) represents an idea inspired by maturational theories of development that plasticity goes through an early period of being consistently high. At some age, plasticity begins to drop off. When full neurocognitive maturation is complete, a floor of sensitivity to environmental variation is reached, at which point no further age effects on acquisition are predicted. (Note, as we saw above, windows of plasticity do not shut suddenly or firmly and some level of plasticity is always retained. The floor level of sensitivity still retains some plasticity. Under a strict notion of critical period, such as that originally conceived to explain filial imprinting in chicks, the floor would represent zero sensitivity to further environmental variation). Figure 2(b) reflects the early phase of heightened plasticity, but then a continuous decline that does not level off. Figure 2(c) represents the idea that from the earliest point measured, plasticity consistently declines. This last function contains no non-linearity: it captures the idea of plasticity reduction without a sensitive period.

Empirical data have been collected to distinguish between these functions in the domain of second language acquisition. In assessing second language learning, one must overcome the confound that individuals learning a language later in life may perform more poorly simply because they have accumulated less experience with the language than if they had been exposed to it from birth. In 1989, Johnson and Newport published data for individuals learning English as a second language beginning at different ages. They measured English language knowledge using a grammaticality judgement task. Participants were tested on 276 sentences, half of which were grammatical and half ungrammatical. The sentences tested a range of syntactic and morphological knowledge. Data were collected for 46 Chinese and Korean learners of English who had arrived in the USA at different ages (from 3 to 39) but who had subsequently lived there for at least five years. The data therefore assessed second language proficiency depending on the age at which acquisition commenced. The five-year limit was intended to minimise differences in accumulated experience by giving all learners a decent period in which to have mastered their second language. Figure 3 (adapted from Birdsong & Molis, 2001, with permission) plots these data (solid symbols). Proficiency appeared to decline with age of arrival between the ages of 5 and 15, but thereafter there was no affect of age of arrival. The pattern, shown with the dashed lines, conforms to that of Figure 2(a), albeit missing the early period of high plasticity. In 2001, Birdsong and Molis published a similar data set, this time for 61 Spanish-speaking immigrants arriving in the USA and once again assessed English proficiency using the same grammaticality judgement test. Figure 3 also contains these data (unfilled symbols). This time, proficiency attained showed no effect of age of arrival for children under 16, but a steady decline in attainment thereafter. The
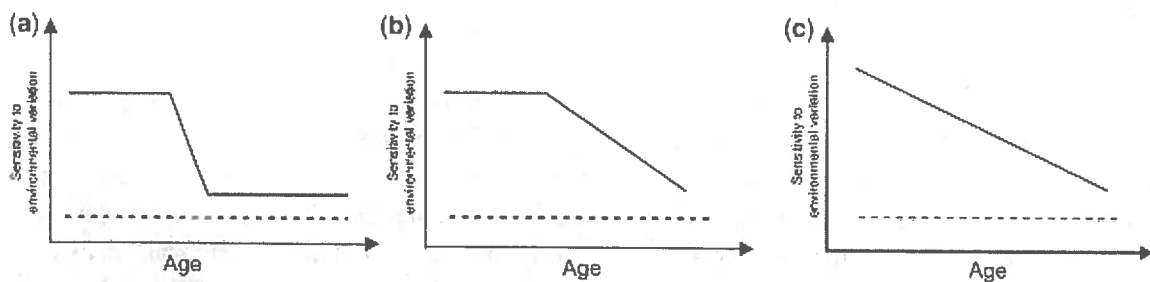

Figure 2. Plots demonstrating the notional sensitivity of a cognitive system to environmental variation across age, for two varieties of a sensitive period (a and b), and a linear decline (c) (see Birdsong, 2005). The dotted line indicates an absence of plasticity.

pattern, shown with the thin black lines, conforms to Figure 2(b). However, if we were to combine these two data sets, the profile can be captured using a single, steadily declining function from the earliest age (thick black line). In short (putting aside the possible confound of accumulated experience), the data unambiguously point to the idea that the later acquisition starts, the lower the proficiency acquired – functional plasticity reduces over time. But the data are ambiguous as to whether the decline is linear or non-linear, that is, whether there is a sensitive period for acquiring a second language or not.

At what age does plasticity decline? The question is in fact difficult to answer, because there is no single thing that is the "plasticity" of cognition. Different functions relating plasticity with age are found for different modalities (e.g., perceptual versus motor skills), for different senses within perception (e.g., vision versus audition), and even for different domains within a single sense (e.g., within vision, different timing of sensitive periods in visual acuity, motion perception, and face perception) (see Huttenlocher, 2002; Johnson, 2005; Neville, 2006, for reviews). Moreover, studies of visual development (see Lewis & Maurer, 2005) have suggested the need to distinguish between sensitive periods for normal development (the timing when visual input is necessary for a normal developmental outcome), sensitive periods for damage (when visual input is necessary to consolidate a skill even when adult levels of functionality have been reached; loss of input can still cause damage in this period), and sensitive periods for recovery (the period
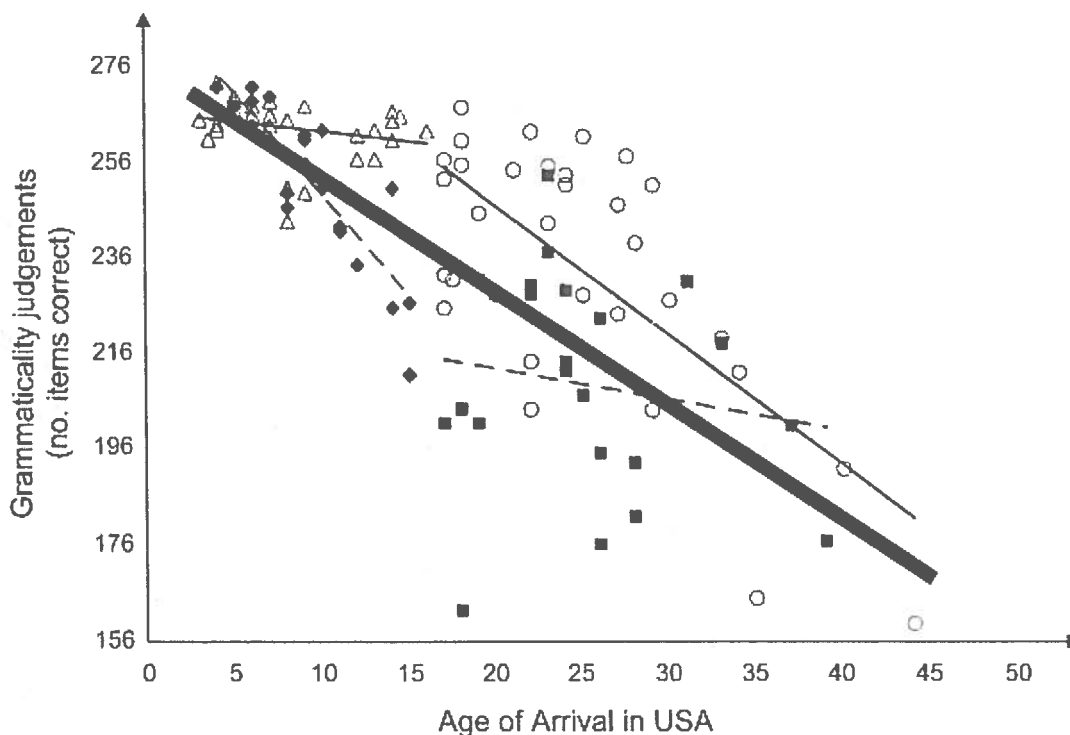

Figure 3. Proficiency of second language acquisition, assessed by a grammaticality judgement task, for learners of English commencing acquisition at different ages depending on when they arrived in the USA. Solid symbols are data from Johnson and Newport (1989) for 46 Korean and Chinese learners of English (diamonds = individuals arriving before age 15, squares = individuals arriving aged 17 or later). Unfilled symbols are data from Birdsong and Molis (2001) for 61 Spanish learners of English (triangles = individuals arriving at or before 16 years of age, circles = individuals arriving at or after 17 years of age). See text for explanation of lines. [Figure adapted from Journal of Memory and Language, 44, D. Birdsong & M. Molis, On the Evidence for Maturational Constraints in Second-Language Acquisition, 235–249, with permission from Elsevier.]

during which the visual system has the potential to recover from the loss of input); each of these aspects may have different timing.

Brain mechanisms might offer some clues with respect to sensitive periods for learning. Synapses are the structures through which neurons communicate. They are initially over-produced in the brain, and the environment selects which ones are retained to support function (see Stiles, 2008, for a review). The density of synapses may be viewed as one measure of the plasticity of the brain, in terms of the potential to alter connection strengths to reflect experience (Huttenlocher, 2002). The combination of initial over-production followed by reduction allows the brain to be flexible early in development (at the cost of maintaining spare resources) and efficient in adulthood (at the cost of reduced flexibility). Huttenlocher and Dabholkar (1997) found that synaptic density in the human brain shows strong increases in the first months and years of life. Synaptic density then subsides during mid-childhood and adolescence. Notably, however, Huttenlocher and Dabholkar found that the age at which synaptic density peaked was different for different regions of the brain. Sensory cortices showed the earliest peaks, while the prefrontal cortex involved in higher cognition showed the latest peak. Cortical grey matter density offers a less direct measure of neural resources and once again, studies suggest that the rate of change is region-specific, with sensory and motor areas showing earliest development and frontal and temporal regions showing the latest development (Gogtay, Giedd, Lusk *et al.*, 2004). Stiles (2008) viewed these data as consistent with a model of brain development moving from the early maturation of primary sensory and motor regions to an ordered elaboration and stabilisation of progressively more complex perceptual and cognitive systems. If measures of synaptic density or grey matter density index plasticity, these data suggest that there is no single thing that is the brain's plasticity. Plasticity is heterogeneous across brain regions at a given point in time.

Lessons for education

What are the lessons for education of these findings from neuroscience? It is important to realise that higher-level behaviours involved in language or music or science or sport are never produced by a single brain area but by networks of co-operating brain areas. Nevertheless, some regions are more heavily implicated in driving a behaviour, or may serve as a limiting factor on behaviour. The broad message is that plasticity reduces earliest in sensory and motor domains and latest in regions associated with higher cognition. Those skills which rely heavily on perceptual discriminations (learning the sounds of a foreign language, hearing music), or which rely heavily on motor skills (gymnastics, playing a musical instrument), are those in which early exposure to the appropriate environment is most important (Huttenlocher, 2002). Three caveats are in order. First, early exposure here typically means mid-childhood, in the approximate range of 5–10. Second, it is currently unclear whether *instruction* is necessary, rather than exposure and spontaneous exploration. Third, at this young age, there may be other factors that limit the level of performance, such as attention and working memory; limiting factors must develop further before high levels of ability can be exhibited (Livesey & Dawson, 1977, 1981).

By contrast, there is much less evidence that plasticity reduces with respect to higher cognition. Therefore, the timing of education for more complex cognitive abilities may be far more flexible. Indeed, there is no strong evidence for age effects in learning literacy and numeracy skills, provided the appropriate perceptual skills are in place. For example, Dehaene, Pegado, Braga, Ventura *et al.* (2010) recently reported that literacy enhanced visual responses in fusiform and occipital cortex, as well as phonological activation to speech in the planum temporale, and that most of these changes occurred even when literacy was acquired in adulthood.

A skill such as language comprises a large number of related tasks, relying differentially on different brain networks. Sensitive periods vary across the components of language (Flege,

Yeni-Komshian, & Liu, 1999; Neville, 2006; Wartenburger, Heekeren, Abutalebi, Cappa, Villringer, & Perani, 2003; Werker & Tees, 2005). Indeed, plasticity shows greater or earlier reductions for phonology and morphology and syntax than it does for lexical semantics, in which there may be no age-related change at all (Slabakova, 2006). The ability to acquire a new language will be the combinatorial result of the relative plasticity of underlying auditory, phonological, semantic, syntactic and motor systems, combined with the developmental interactions between these components. Where systems interact, the earliest committing, least plastic system may become the limiting factor on change. Thus when individuals attempt to learn languages later in life, an attenuated ability to distinguish the component sounds of the language (or in the case of sign language, hand shapes) may be the limiting factor on the rate of acquisition and level of ultimate proficiency (McDonald, 1997). Less marked impairments in morphology and grammar may turn out to be the result of difficulties representing the input signal, which then affect the computations that must be carried out on this signal quickly and automatically to achieve fluency.

Lastly, there are clear examples of the brain learning itself into situations it can't get out of, so to speak. Literacy and numeracy represent cases where extended instruction serves to integrate existing sub-systems of the brain into novel functional structures. For reading, the visual system must be integrated with the existing spoken language system. Dyslexia can stem from problems representing phonology (the speech sounds) of a language. To maximise protection against dyslexia in children who are at risk of the disorder through family background, researchers found that problems with phonology need to be alleviated *before* children learned to read (Bus & Ijzendoorn, 1999). Once the children started to learn associations between written letters and poorly structured phonology, this learning was harder to undo (Harm, McCandliss & Seidenberg, 2003). For numeracy, three systems must be integrated. These include an attention system for simultaneously following a small number of objects (later used for "subitising" or instantly counting small numbers of items), a spatial system for processing analogue magnitudes (e.g., to estimate amounts), and language-based system for representing number words, sequences and facts such as times tables (Carey & Sarnecka, 2006). The number words of the child's first language are integrated into a larger, emerging number system. Once this system is formed, if children or adults subsequently learn another language (even to a higher level of competence, with the first language decaying), the first-learned language cannot be readily "unplugged" from its role in encoding number facts – adult bilinguals generally find they have to resort to their first acquired language for mental arithmetic (Wang, Lin, Kuhl & Hirsch, 2007).

How do you learn if plasticity has been reduced?

Plasticity rarely if ever disappears. The adult may have to work harder to learn, deploying more cognitive resources (Knusden, 2004), and may not reach the same level of performance. This is not inevitable, however: under certain circumstances, older learners can develop new skills more quickly than their younger counterparts because of the additional strategies available to them (DeKeysar & Larson-Hall, 2005). Moreover, the example of second language acquisition did not reveal an age beyond which a floor of plasticity was reached. Instead, the evidence pointed to a linear decline: the later you start to learn a second language, the lower your final level is likely to be (Birdsong, 2006).

The study of language learning also suggests that adults and children learn in different ways. Children are implicit learners, they are relatively insensitive to feedback, and extract regularities from exposure to large amounts of input; by contrast, adults adopt explicit strategies and remain responsive to feedback, so that a single counter example can cause the individual to revise his or

her knowledge (Hudson Kam & Newport, 2005). Table 1 lists several characteristics that distinguish children's and adults' learning. For the young child, learning often occurs automatically and implicitly via exploration, occurring in many domains simultaneously through natural exposure. For the adult, intense training may be required with the cessation of other tasks, the exaggeration of key dimensions of the target domain, and the use of explicit strategies, with motivation also important. But in some regards, the adult and child learner will be the same. For instance, both may require attention to learn (see, for example, Schmidt, 1995). Animal research also points to the importance of a social context to enhance learning, likely to hold for children and adults alike but particularly valuable for the adult to enhance plasticity (e.g., one study indicated that at an age songbirds were too old to learn their song from a passive tape-recording because of a closing sensitive period, they could still do so from an interactive partner; Jones, Ten Cate, & Slater, 1996).

While early and mid-childhood are often emphasised as a time of heightened functional plasticity, it is important to note that, at least with regards to educational achievement, the brain retains significant plasticity in the teenage years. For example, Ramsden and colleague (2011) recently examined teenagers' verbal and visuospatial abilities, as assessed by standardised intelligence tests, following up a group of 35 individuals after a three and a half year gap from early to late adolescence. Those individuals who had improved on their vocabulary showed a region-specific increase in grey matter in the supramarginal gyrus, while those who had improved on their visuospatial ability showed a region-specific increase in grey matter in the left superior parietal lobe (against, recall, a global decrease in grey matter depicted in Figure 1). These data could not distinguish whether these effects were genetic (the late unfolding of potential) or environmental (the effects of educational training). They were, however, suggestive that the individual's potential is not fixed by mid-childhood but may still emerge through adolescence, and that this emergence is underpinned by localised changes in brain structure. Indeed, research within cognitive neuroscience is also increasingly focusing on how puberty may affect cognitive abilities in adolescence (Blakemore & Choudhury, 2006; Giedd, Clasen, Lenroot *et al.*, 2006). The teenage years are in many respects crucial for children's educational achievement and research indicates plenty of scope for brain plasticity to support skill acquisition.

Extending to a lifespan perspective, one can also consider how plasticity might reduce in ageing, in line with a decline in cognitive abilities. In a recent review of this literature, Hertzog, Kramer, Wilson and Lindenberger (2009) concluded that the longitudinal evidence consistently shows that engaging in intellectually stimulating activities is associated with better cognitive functioning. Two other beneficial factors were also apparent: the importance of social engagement and of aerobic exercise in protecting against cognitive decline. By contrast, stress and psychological distress are risk factors for decline. Figure 1 similarly reflects changes in the brain, with global white matter beginning to decline in older individuals (recall, very broadly, white matter might be thought to index established knowledge and skills). Inasmuch as we have considered the relationship between functional plasticity and age as indicating optimal timing for cognitive stimulation to drive skill *acquisition* in childhood, in later adulthood that same stimulation is required for skill *retention*.

Individual differences in plasticity

Are there individual differences in brain plasticity, and can these be related to differences in cognitive ability? Researchers have begun to address this question by exploring changes in cortical thickness with age. The micro-level changes that produce thickening or thinning of the cerebral cortex are not completely understood, but thickening is likely to reflect growth

Table 1. Different characteristics of learning in children and adults

Child Learner	Adult Learner
Exploration	Intense training
Many tasks at once	Cease interfering tasks
Natural exposure	Exaggerate key dimensions
Attention	Attention + motivation
Implicit learning	Use of explicit strategies
Social context enhances learning	Social context enhances learning

in connectivity, as well as the blood vessels, fibres and surrounding glial cells that support the function of neurons, although not the growth of new neurons themselves, while thinning is likely to reflect myelination and synaptic pruning. Shaw, Greenstein, Lerch, Clasen *et al.* (2006) examined changes in cortical thickness in children between 7 and 19 years of age and found that children with higher IQs showed greater thickening and then faster thinning than children with lower IQs. Differences in ability were marked by different trajectories of change rather than absolute differences in cortical thickness. Brans, Kahn, Schnack, van Baal *et al.* (2008) examined young adults and found somewhat surprisingly that certain brain regions were still showing thickening and thinning in the 20s and 30s that were associated with differences in ability. In this case, higher IQ individuals were marked by a pattern of faster thickening in the regions where thickening was observed, but slower thinning where thinning was observed, compared to adults with lower IQs. A comparison of the studies of Shaw *et al.* and Brans *et al.* suggests that cortical thinning in childhood reflects optimisation, while cortical thinning in adulthood reflects loss.

Brans *et al.*'s (2008) study employed twin pairs and was therefore able to assess genetic versus environmental contributions to individual differences in both brain structure and intelligence. The results indicated strong genetic influence for both, and also that there was overlap in the genes that influenced variability in intelligence and variability in brain plasticity. About half the variability in each measure, however, was of unique environmental origin. Part of this environmental effect, presumably, corresponded to the effect of education.

The interplay of genetic and environmental factors in brain plasticity was highlighted in a recent study by Golestani, Price, and Scott (2011), who studied brain structure in expert phoneticians, that is, individuals who are highly trained to analyse and transcribe speech. Golestani *et al.* found a positive correlation between the size of one brain structure (the left pars opercularis) and the number of years of phonetic transcription training that the individual had undertaken. This finding illustrates the role of experience and the operation of plasticity in shaping brain structures. However, the expert phoneticians were also found to be more likely than controls to have multiple or split left transverse gyri (a characteristic of the folding of the cortex). This structural property is established in utero. Therefore, the implication of the study is that this folding property conveyed a benefit in learning to process speech, which then affected subsequent career choice. In other words, these individuals began with a certain potential, but the potential had to be realised by training.

How can brain plasticity be enhanced?

There are two current streams of research investigating how brain plasticity might be enhanced. The first investigates how learning may be optimised in humans, while the second seeks to manipulate the brain mechanisms of plasticity directly and is typically carried out with animals.

The human research mostly focuses on changes in information processing and its efficiency, while animal studies characterise the molecular and cellular mechanisms that allow changes in connectivity (Bavelier *et al.*, 2010).

Studies of learning often focus on adults where, as we have seen, learning capacities have reduced or changed in their nature. Studies of perceptual learning suggest that certain properties of the training environment need to be optimised for best outcome (Green & Bavelier, 2008). These include adjusting the difficulty of the task so that it is always just in advance of the individual's current level, ensuring that the learner has the appropriate motivational state, and offering the appropriate type of feedback. One of the key issues is the extent to which training-induced learning offers general benefits, rather than improvement solely on the task itself, and so implicating a more general effect on brain plasticity. Activities that show promise in enhancing learning are perhaps surprising: they included playing action video games (Green, Li & Bavelier, 2010), musical training (Habib & Besson, 2009; Wan & Schlaug, 2010), athletic training (Kioumourtzoglou, Kourtessis, Michalopoulou, & Derri, 1998), and aerobic fitness training (Kramer & Erickson, 2007; see Green & Bavelier, 2008, for a review).

With regard to action video games (putting aside the content of the games), these are argued to offer benefits because of the varied skills that they require, the engrossing and rewarding nature of the activity, the demands for split attention and efficient reallocation of attentional resources as task demands change, and the sense of deep engagement and control engendered by the immersive environment (Bavelier *et al.*, 2010). However, where an activity like video gaming produces improvements in perceptual skills, the current suggestion is that these gains arise from changes in top-down attentional processes (i.e., how the brain uses its perceptual information) rather than reaching down to rewire the senses themselves. Consistent with the story we have seen thus far, the greater residual plasticity is in higher level cognitive skills. Musical training is argued to be of general benefit because of the highly practised association of motor actions with specific sound and visual patterns, along with continuous multisensory feedback. This combination is argued to strengthen connections between auditory regions, motor regions, and multimodal integration regions, and to lead to enhanced plasticity of these pathways (Wan & Schlaug, 2010). However, for both action video games and musical training, researchers are yet to gain a full understanding of the mechanistic basis of observed behavioural advantages.

Animal studies of the mechanisms of plasticity indicate that multiple molecular mechanisms have evolved to allow the optimal timing and duration of plasticity and so ensure an adaptable yet efficient organism (Bavelier *et al.*, 2010). Bavelier *et al.* recently characterised the "brakes" on plasticity that underpin the consolidated adult state. These include structural brakes that restrict local connectivity changes, and functional changes that regulate the plastic potential of established neural networks (such as the balance between excitation and inhibition). Animal studies have explored the potential to "release" some of these brakes with neuromodulatory drugs, which may for instance alter the excitation-inhibition balance. Such direct pharmacological manipulations of brain plasticity have a risk attached, in that consolidated knowledge may be lost. Research is therefore likely to be restricted initially to exploring ways to enhance recovery after strokes. For educational purposes, environmental manipulations that enhance skill learning are the most promising. It may be that such techniques turn out to operate via the mechanisms identified in the animal studies. For instant, the right level of task challenge, immersion, motivation and reward to enhance learning may result in neuromodulatory changes that alter the excitation-inhibition balance in neural networks (see Bavelier *et al.*, 2010, for a review).

Summary and conclusion

Changes in functional plasticity – that is, our ability to change behaviour through experience – with increasing age are gradual, not sudden. A large body of work has explored how changes in functional plasticity may be related to the properties of the brain, in terms of the mechanisms delivering changes in behaviour. Sensitive periods, where there is an early period of heightened plasticity, have been studied predominantly in the context of perceptual skills. There are many different types of sensitive period in perception. However, there is little evidence of particular sensitive periods for higher cognitive abilities relevant to education, such as literacy and numeracy (unless these abilities rely on low-level perceptual skills, as may be the case with second language learning). Neuroscience therefore offers less of a constraint on the timing of when higher cognitive skills should be taught; other factors should be considered in making curriculum-based decisions. Nevertheless, the overall picture is of a slow decline in plasticity with increasing age, and a change in learning style from childhood to adulthood. The teenage years represent an intermediate case and are a focus of current research.

Research in neuroscience indicates that there is no such thing as *the* brain's plasticity: age-related changes in the structural properties of the brain, such as synaptic density, cortical thickness, and the amount of grey matter, turn out to be region specific, implying that different brain areas have different trajectories of plasticity change with age. There may be individual differences in brain plasticity that relate to differences in intellectual ability, but research in this area is in its early stages. The emerging picture is of a complex interplay of genetic and environmental factors. Recent research on how to enhance plasticity (of particular relevance in adulthood) has identified the properties that training tasks must have to lead to general benefits in learning, involving the appropriate combination of task difficulty, engagement, motivation, and feedback. The tasks that show most promise (action video gaming, musical training, sports training, and aerobic exercise) suggest future directions for the design of balanced curricula in education.

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