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Address for correspondence:

Dr. Michael Thomas
Developmental Neurocognition Laboratory
School of Psychology
Birkbeck College, University of London
Malet Street, Bloomsbury
London WC1E 7HX, UK
Email: m.thomas@bbk.ac.uk
http://www.bbk.ac.uk/psyc/staff/academic/mthomas
www.psyc.bbk.ac.uk/research/DNL/
Tel.: +44 (0)20 7631 6386
Fax: +44 (0)20 7631 6312

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New advances in understanding sensitive periods in brain development

Michael S. C. Thomas and Mark H. Johnson

School of Psychology, Birkbeck, University of London, London, UK

Abstract

Is a dog ever too old to learn new tricks? We review recent findings on sensitive periods in brain development, ranging from sensory processing to high-level cognitive abilities in humans. We conclude that there are multiple varieties of, and mechanisms underlying, these changes. However, many sensitive periods may be a consequence of the basic processes underlying postnatal functional brain development.

Key words: Sensitive Periods, learning, plasticity

Introduction

The idea that there are "critical" or sensitive periods in neural, cognitive and behavioural development has a long history, and first became widely known with the phenomenon of *filial imprinting* as famously described by Konrad Lorenz. 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 (see Figure 1). According to Lorenz, a critical period in development has several features including that learning or plasticity is confined to a short and sharply defined period of the life cycle, and that this learning is subsequently irreversible in the face of later experience. Following the paradigmatic example of filial imprinting in birds, more recent studies on cats, dogs, monkeys, bird song and human language development, have confirmed that critical periods are major phenomena in brain and behavioural development (see Michel & Tyler, 2005, for review). However, even with imprinting, the prototypical example of a critical period, it rapidly became evident that these periods were not as sharply timed and irreversible as first thought. For example, the critical period for imprinting in domestic chicks was shown to be extendable in time in the absence of appropriate stimulation, and the learning is reversible under certain circumstances (for review, see Bolhuis, 1991). These and other modifications of Lorenz's original views have led most current researchers to adopt the alternative term "sensitive periods" (SP) to describe these widespread developmental phenomena.

A fundamental debate that continues to the present is whether specific mechanisms underlie sensitive periods, or whether SPs are a natural consequence of functional brain development. Support for the latter view has come from a recent perspective on developing brain functions.

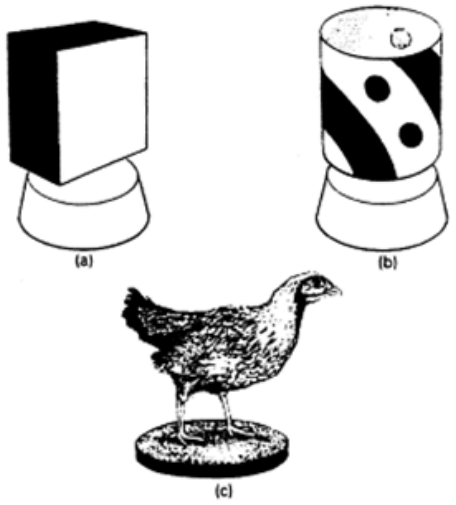

Figure 1: Examples of three stimuli used to study visual imprinting in the domestic chick. Chicks are hatched and reared in darkness before being exposed to the visual stimulus. Training usually lasts for a period of several hours. Hours or days later, the chick is released in the presence of two objects, one to which it was exposed earlier and a novel object. If the chick has imprinted strongly, it will show a high preference for the familiar object by approaching it.

Relating evidence on the neuroanatomical development of the brain to the remarkable changes in motor, perceptual, and cognitive abilities during the first decade or so of a human life presents a formidable challenge. A recent theory, termed "Interactive Specialisation" argues that postnatal functional brain development, at least within cerebral cortex, involves a process of increasing specialisation, or fine-tuning, of response properties (Johnson, 2001, 2005). According to this view, during postnatal development changes in the response properties of cortical regions occur as they interact and compete with each other to acquire their role in new computational abilities. That is, some cortical regions begin with poorly defined functions and consequently are partially activated in a wide range of different contexts and tasks. During development, activity-

dependent interactions between regions sharpen up their functions, such that their activity becomes restricted to a narrower set of stimuli or task-demands. For example, a region originally activated by a wide variety of visual objects may come to confine its response to upright human faces. The termination of SPs is then a natural consequence of the mechanisms by which cortical regions become increasingly specialised and finely tuned. Once regions have become specialised for their adult function, this commitment is difficult to reverse. If this view is correct, sensitive periods in human cognitive development are intrinsic to the process that produces the functional structure of the adult brain.

In order to better understand how sensitive periods relate to the broader picture of vertebrate functional brain development, researchers have addressed a number of specific questions. In any given species are there multiple SPs or just a few (e.g., one per sensory modality)? If there are multiple SPs, do these share common underlying mechanisms? What are the processes that underlie the end of SPs and the corresponding reduction in plasticity?

Varieties of Sensitive Period

Recent work indicates that there are multiple SPs in the sensory systems that have been studied. For example, within the auditory domain there are different SPs for different facets of speech processing, and other SPs with different timing related to basic aspects of music perception in humans. Similarly, in primate visual systems there are, at a minimum, different SPs related to amblyopia, visual acuity, motion perception, and face processing (see Johnson, 2005, for review).

How do these different and varied sensitive periods relate to each other? While this is still poorly understood, high-level skills like human language involve the integration of many lower-level systems. Plasticity in language acquisition is therefore likely to 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. The literature currently available suggests that plasticity tends to reduce in low-level sensory systems before it reduces in high-level cognitive systems (Huttenlocher, 2002).

While it is now agreed that there are multiple SPs even within one sensory modality in one species, there is still considerable debate as to whether these different sensitive periods reflect common underlying mechanisms, or whether different mechanisms and principles operate in each case.

Mechanisms underlying Sensitive Periods

A major feature of SPs is that plasticity appears to be markedly reduced at the end of the period. There are three general classes of explanation for this: (1) endogenous termination due to maturation, (2) learning is self-terminating, and (3) underlying plasticity does not actually reduce but the constraints on plasticity become stable.

According to the first view, *endogenous changes in the neurochemistry of the brain region* in question could increase the rate of pruning of synapses resulting in the "fossilization" of existing patterns of functional connectivity. Thus, the termination of sensitive periods would be due to endogenous factors, have a fixed time course, and could be specific to individual regions of cortex. Empirical evidence on neurochemical changes associated with plasticity, such as expression of glutamatergic and GABA receptors in human visual cortex, indicate that the periods of neurochemical change can occur around the age of functional sensitive periods (see Figure 2). However, this does not rule out the possibility that these neurochemical changes are a consequence of the differences in functional activity due to termination of plasticity, rather than its cause (Murphy et al. 2005).

The second class of mechanism implies that SPs involve *self-terminating learning processes*. By self-terminating, we mean that the process of learning itself produces changes that reduce the system's plasticity. These types of mechanisms are most consistent with the view of SPs as a natural consequence of typical functional brain development. An important way to describe and understand self-terminating learning comes from the use of computer-simulated neural networks (Thomas & Johnson 2006). These models demonstrate mechanistically how processes of learning can lead to neurobiological changes that reduce plasticity, rather than plasticity changing according to a purely maturational timetable. Such computers models have revealed that even where a reduction in plasticity emerges with increasing experience, a range of different specific mechanisms may be responsible for this reduction (see Thomas & Johnson, 2006). For example, it may be that the neural system's computational resources, which are critical for future learning, have been claimed or used up by existing learning, so that any new learning must compete to capture these

resources. Unless earlier learned abilities are neglected or lost, new learning may always be limited by this competition. Another mechanism discovered through modelling is called “entrenchment”. In this case, prior experience places the system into a state that is non-optimal for learning the new skill. It takes time to reconfigure the system for the new task and learning correspondingly takes longer than it would have done had the system been in an uncommitted state. A third mechanism is assimilation, where initial learning reduces the system’s ability to detect changes in the environment that might trigger further learning.

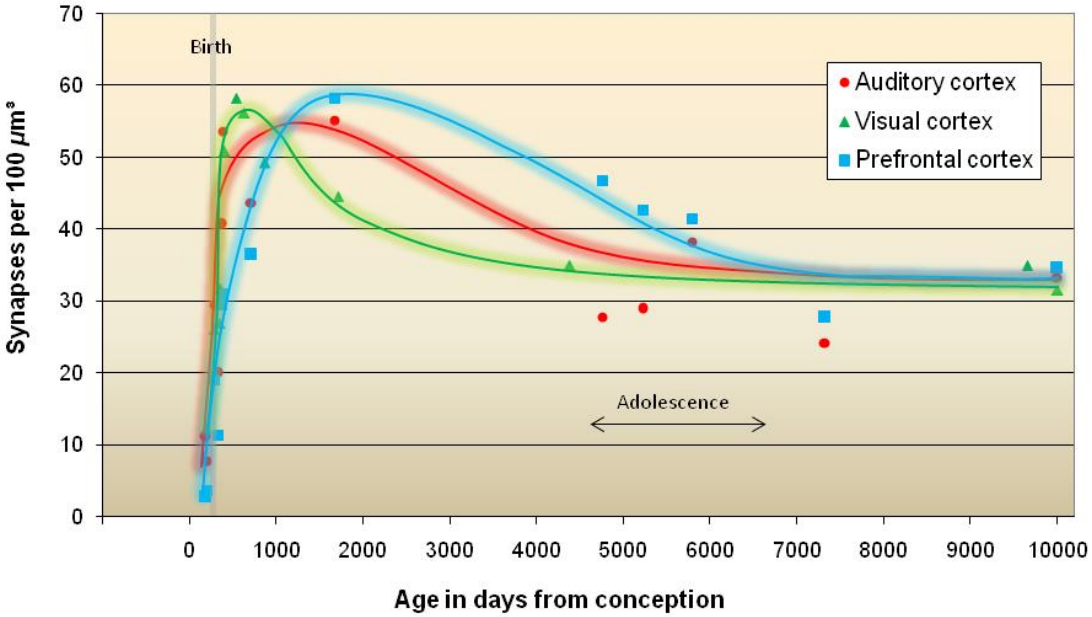

Figure 2: Synapses are the structures through which neurons communicate. Synaptic density provides one measure of the strength of functional connectivity between neurons. Synapses are initially overproduced in the brain and the environment selects which ones are retained to support function. The density of synapses may be viewed as one measure of the plasticity of the system – the potential to alter connection strengths to reflect experience (Huttenlocher, 2002). Measures of synaptic density indicate that: (a) there is a strong initial increase, which later subsides during mid-childhood and adolescence; and (b) the synaptic density function peaks at different times in different regions of the brain. Notably, prefrontal cortex (middle frontal gyrus), a region associated with higher-level cognition, shows the latest peak in synaptic density. (Adapted from Huttenlocher & Dabholkar, 1997).

Evidence from humans relevant to self-terminating SPs is reported by Lewis and Maurer (2005) who have studied the outcome of cases of human infants born with dense bilateral cataracts in both eyes. Such dense bilateral cataracts restrict these infants to near blindness, but fortunately the condition can be rectified with surgery. Despite variation in the age of treatment from 1 to 9 months, immediately following surgery to remove the cataracts, infants were found to have the visual acuity of a newborn. However, after only *one hour* of patterned vision, acuity had improved to the level of a typical 6-week old, and after a further month of visual experience the gap to age-matched controls was very considerably reduced. These findings correspond well with animal experiments showing that dark-rearing appears to delay the end of the typical sensitive period. Thus, in at least some cases, plasticity seems to wait for the appropriate type of sensory stimulation. This is consistent with the idea that changes in plasticity can be driven by the learning processes associated with typical development.

Returning to the paradigmatic example of filial imprinting in birds, O'Reilly and Johnson (1994) constructed a computer model of the neural network known to support imprinting in the relevant region of the chick brain. This computer model successfully simulated a range of phenomena associated with imprinting behaviour in the chick. Importantly, in both the model and the chick, the extent to which an imprinted preference for one object can be "reversed" by exposure to a second object depends on a combination of the length of exposure to the first object and the second object (for review, see Bolhuis, 1991). In other words, the sensitive period was dependent on the respective levels of learning and was self-terminating. Additionally, like the chick, the network *generalised* from a training object to one that shares some of its features, such as colour or shape. By gradually changing the features of the object to which the chick was exposed, its preference could be shifted even after the "sensitive period" had

supposedly closed. The simulation work demonstrated the sufficiency of simple learning mechanisms to explain the observed behavioural data (McClelland, 2005).

The third class of explanation for the end of SPs is that it represents the onset of *stability in constraining factors* rather than a reduction in the underlying plasticity. For example, while an infant is growing the distance between her eyes increases, thereby creating instability in the information to visual cortical areas. However, once the inter-eye distance is fixed in development, the visual input becomes stable. Thus, brain plasticity may be "hidden" until it is revealed by some perturbation to another constraining factor that disrupts vision.

This mechanism potentially offers an attractive explanation of the surprising degree of plasticity sometimes observed in adults, for instance after even quite short-lasting visual deprivation. Using this technique, Sathian (2005) has reported activity in visual cortex during tactile perception in sighted human adults, similar to that observed in those who have suffered long-term visual deprivation. While this line of research initially appears consistent with life-long plasticity, it is important to note that this tactile-induced visual cortex activity is much greater if vision is lost early in life or was never present. Thus, although there appears to be residual connectivity between sensory systems that can be uncovered by blocking vision in sighted people, there is also a sensitive period during which these connections can be more drastically altered.

Sensitive Periods in Second Language Acquisition

Given the variety of mechanisms that may underlie SPs, it is of interest to ask how SPs impact on the acquisition of higher cognitive abilities in humans. Recent work on learning a second language provides an interesting example. If you want to master a second language, how important is the age at which you start to learn it? If you start to

learn a second language as an adult, does your brain process it in a different way to your first language?

It is often claimed that unless individuals acquire a second language (L2) before mid-childhood (or perhaps before puberty), then they will never reach native-like levels of proficiency in the second language in pronunciation or grammatical knowledge. This claim is supported by deprivation studies showing that the acquisition of a first language (L1) is itself less successful when begun after a certain age. Further, functional brain-imaging studies initially indicated that in L2 acquisition, different areas of cortex were activated by the L2 compared to the L1; only in individuals who had acquired two languages simultaneously were common areas activated (e.g., Kim et al., 1997).

However, subsequent research has painted a more complex picture. First, claims for SPs rely on assessing *final level of attainment* rather than *speed of learning*. This is because there is evidence that adults can learn a second language more quickly than children, even if their final level of attainment is not as high. Indeed adults and children appear to learn a new language in different ways. Children are relatively insensitive to feedback and extract regularities from exposure to large amounts of input, while adults adopt explicit strategies and remain responsive to feedback (see, e.g., Hudson Kam & Newport, 2005).

Second, even when the final level of L2 attainment is considered, it has proved hard to find an age after which prospective attainment plateaus. That is, there is no strong evidence for a point at which an SP completely closes (see, e.g., Birdsong, 2006). Instead, L2 attainment shows a linear decline with age: the later you start, the lower your final level is likely to be (Birdsong, 2006).

Third, recent functional imaging research has indicated that at least three factors are important in determining the relative brain activation patterns produced by L1 and L2 during comprehension and production. These are the age of acquisition, the level of usage/exposure to each language, and the level of proficiency attained in L2. Overall, three broad themes have emerged (Abutalebi et al., 2005; Stowe & Sabourin, 2005): (i) the same network of left hemisphere brain regions is involved in processing both languages; (ii) a weak L2 is associated with more widespread neural activity compared to L1 in production (perhaps because L2 is effortful to produce) but less activation in comprehension (perhaps because L2 is less well understood); and (iii) the level of proficiency in L2 is more important than age of acquisition in determining whether L1 and L2 activate common or separate areas. In brief, the better you are at L2, the more similar the activated regions are to L1. This finding fits with the idea that certain brain areas are optimised for processing language (perhaps during the acquisition of L1) and in order to become very good at L2, you have to engage these brain areas. The idea that later plasticity is tempered by the processing structures created by earlier learning fits with the Interactive Specialisation explanation for the closing of SPs.

Finally, in line with idea that language requires integration across multiple sub-skills, increasing evidence indicates that SPs differ across the components of language (Neville, 2006; Wartenburger et al., 2003; Werker & Tees, 2005). Plasticity may show greater or earlier reductions for phonology and morphosyntax than it does for lexical-semantics, in which there may indeed be no age-related change at all. Thus, for the late language learner, new meanings are easier to acquire than new sounds.

Conclusion

It is important to understand the mechanisms underlying SPs for practical reasons. Age-of-acquisition effects may shape educational policy and the time at which children are exposed to different skills. The reversibility of effects of deprivation on development has important implications for interventions for children with congenital sensory impairments or children exposed to impoverished physical and social environments. And there are clinical implications for understanding the mechanisms that drive recovery from brain damage at different ages.

Exciting vistas for the future include using genetic and brain imaging data to identify the best developmental times for training new skills in individual children, and a deeper understanding of the neurocomputational principles that underlie self-terminating plasticity may allow for more efficient design of training procedures (McClelland 2005).

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