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New advances in understanding sensitive periods in development

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Abstract

Is a dog ever too old to learn new tricks? We review recent findings on sensitive periods in brain development, ranging from sensory to high-level cognitive abilities. We conclude that changes in our ability to adapt to the environment over time are not clear-cut, and that there are multiple mechanisms underlying these changes. However, progress in understanding the basic processes of functional brain development is generating increasing insights into sensitive periods.

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. 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. 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.

Recent theoretical and empirical progress in the study of sensitive periods has been achieved through a greater understanding of the way in which mechanisms of brain development constrain cognitive development and new learning. New techniques in brain imaging, large-scale behavioural studies, and neural network modelling of brain plasticity have all contributed to our understanding of people's ability to modify their behaviour and how this changes with age. In this article, we will review recent advances in our understanding of sensitive periods and address the following questions. In any given species are there multiple SP's or just a few (e.g., one per sensory modality)? If there are multiple SP's, do these share common underlying mechanisms? What are the processes that underlie the end of SP's and the corresponding reduction in plasticity? And finally, how do SP's fit in to the broader picture of human functional brain development?

Varieties of Sensitive Period

Recent work forces the conclusion that there are multiple SP's in the sensory systems under study. For example, within the auditory domain there are different SP's for different facets of speech processing, and other SP's with different timing related to basic aspects of music perception in humans. Similarly, in primate visual systems there are, at a minimum, different SP's related to amblyopia, visual acuity, motion perception, and face processing (see Johnson, 2005, for review). Further, SP's in different sensory modalities do not appear to correspond in their time course, and can have quite different consequences for later functioning. For example, while early unilateral brain damage can lead to long-term deficits in face processing, it tends to effect language acquisition much less (see later). Taken together, these recent findings indicate that there are multiple and variable types of SP's during human development.

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). Understanding the success or failure of learning at different ages becomes complicated because on the one hand, reduced plasticity in lower-level systems may be a limiting factor on acquiring a cognitive skill, while on the other hand, there may be alternative ways to successfully acquire a high-level skill as the plasticity of various sensory and perceptual systems reduces.

While it is now agreed that there are multiple SP's 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. This is the question that we now address.

Mechanisms underlying Sensitive Periods

While SP's are easy to describe, it has proved far more challenging to reveal and understand the underlying mechanisms. In part, this is because the idea has been invoked to explain at least three different types of phenomena with regard to human development: (1) the speed (or final level) of learning for tasks first encountered at different ages; (2) the effects of early deprivation on subsequent development; and, (3) the ability of individuals to recover from brain damage experienced at different ages. Thus, it is commonly thought that children need to start learning certain skills at an early age in order to achieve maximum mastery of that skill, such as speaking a second language or acquiring absolute pitch perception (e.g., Trainor, 2005). The study of children who are deprived of visual input due to congenital cataracts indicates that unless normal input is restored within the first few weeks or months of life, certain visual capacities may never be learned normally. These include the perception of motion and orientation, and even some aspects of face recognition (Maurer, Lewis, & Mondloch, 2005). And a comparison of recovery profiles for language following unilateral left hemisphere brain damage indicates that children who experience this damage prior to around 7 years of age show much better recovery compared to adults who experience the same damage; indeed, the children sometimes recover to within the normal range of language ability while the adults suffer persistent aphasia.

It is important to understand the mechanisms underlying each of these human developmental phenomena 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.

One place to start in uncovering the mechanisms that underlie SP's is to focus on what causes the periods to end.

The Termination of Sensitive Periods

A major feature of SP's 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. In addition to direct empirical evidence, research in computer modelling of neural networks can be used to explore the potential mechanisms underlying changes in plasticity, and to refine specific hypotheses (Thomas & Johnson, 2006).

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. In order to investigate in more detail how such a mechanism for terminating plasticity might work, a number of investigators have run computer simulations with simple network models of the cortex that undergo phases of connection loss similar to the synaptic pruning seen during real postnatal development. These simulations illustrate how reductions in plasticity could arise from changes in neurochemical or trophic factors in specific locations of the brain at particular times. 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 most rapid neurochemical change occur well after the age of functional sensitive periods. This is inconsistent with strict maturational regulation of levels of plasticity and is more consistent with the continuation of a lower level of plasticity, or the view that these neurochemical changes are a consequence of the differences in functional activity due to termination of plasticity rather than its cause.

Moving on to the second class of mechanism, one possibility is that SP's involve *self-terminating learning processes*. Once again, computer simulated neural networks have been used to illustrate candidate mechanisms. These models show how learning can lead to neurobiological changes that reduce plasticity, rather than plasticity changing according to a purely maturational timetable. In a sense, learning drives the system into a cul-de-sac. 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 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 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.

Evidence from humans relevant to self-terminating SP's is reported by Lewis and Maurer (2005) who have studied the outcome of cases of 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 learning itself.

Returning to the paradigmatic example of filial imprinting in birds, O'Reilly and Johnson's (1994) constructed a computer model of the neural network that supports imprinting in the relevant region of the chick brain. This computer model successfully simulated a range of phenomena associated with imprinting 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 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 third class of explanation for the end of SP's 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. Available plasticity may be "hidden" until it is revealed by some perturbation to another constraining factor that disrupts vision.

This latter class of mechanism potentially offers an attractive explanation of the surprising degree of plasticity sometimes observed in adults, for instance even after quite short-lasting visual deprivation. Using this technique, Sathian (2005) has reported activity in visual cortex during tactile perception in both sighted human adults as well as 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 revealed 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

How do SP's impact on the acquisition of higher cognitive abilities? Recent work on learning a second language provides an interesting example. If you want to master a second language, how important is it at what age 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?

On the face of it, second language (L2) acquisition seems to represent a good example of an SP in human development. It has been suggested that unless individuals acquire a second language before mid-childhood (or perhaps before puberty), then they will never reach native-like levels of proficiency in the second language, for example in pronunciation or grammatical knowledge. The 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, e.g., in deaf children not initially exposed to sign language. Moreover, functional brain-imaging studies initially indicated that in L2 acquisition, different areas of cortex were activated by the L2 compared to the L1, particularly in left frontal areas; only in individuals who had acquired both languages simultaneously were common areas activated (e.g., Kim et al., 1997).

However, subsequent research has painted a more complex picture. First, claims for SP's 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 has high. Indeed, in some respects, adults and children appear to learn a new language in different ways. The children are relatively insensitive to feedback and extracting regularities from exposure to large amounts of input, while the 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 a period closes (see, e.g., Birdsong, 2006). Instead, the function linking final level of L2 attainment with age of acquisition is closer to a linear decline: the later you start, the lower your final level is likely to be (see Birdsong, 2006, for discussion of individuals who appear to be exceptions to this rule). A linear decline includes no discrete *period* of heightened plasticity for language learning.

Third, subsequent 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 in L2. Overall, three broad themes have emerged (Abutalebi et al., 2005; Stowe & Sabourin, 2005): (i) the same network of left hemisphere perisylvian regions is involved in processing both languages; (ii) a weak L2 is associated with more widespread 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. 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 via the acquisition of L1) and in order to become very good at speaking and understanding L2, you has to employ these brain areas.

Finally, in line with idea that language is a high-level ability that integrates across multiple sub-skills, increasing evidence has accumulated that the function relating plasticity to age differs across the components of language. Plasticity may show greater or earlier reductions for phonology and morphosyntax than it does for lexical-semantics, in which there may be no age-related reduction at all. For the late language learner, new meanings are easier to acquire than new sounds.

Sensitive Periods as part of Human Functional Brain Development

In sum, the general weight of the evidence we have discussed indicates that SP's in development are firstly multiple and various, and secondly, often self-terminating. How can these properties fit together with other aspects of functional brain development? 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. We finish with one recent perspective on this question, called the "interactive specialization" theory. This theory argues that postnatal functional brain development, at least within cerebral cortex, involves a process of increasing specialisation of response properties (Johnson, 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 SP's 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.

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