Review

Perceptual learning and sensomotor flexibility: cortical plasticity under attentional control?

Manfred Fahle^{1,2,*}

¹*Human Neurobiology, Bremen University, 28211 Bremen, Germany*

²*The Henry Wellcome Laboratories of Vision Sciences, City University London, London EC1V 0HB, UK*

Recent research reveals long-lasting cortical plasticity of early sensory cortices even in adults. Sensory signals could be modified under top-down control if necessary quite early in order to optimize their signal-to-noise ratio, leading to ‘low level’ or ‘early’ perceptual learning (PL). For easy tasks, such elaborate top-down influences are usually not required, and learning is restricted to late selection of the appropriate signals on higher cortical levels, which seems easier and faster to achieve. But to reach the absolute limits of sensory performance, PL seems to optimize the entire chain of sensory processing. Hence, improvement for these extreme perceptual abilities is quite specific for a number of stimulus parameters, such as the position in the visual field and sometimes even the trained eye, reflecting the specificity of receptive fields in early sensory cortices. Early PL may be just one example—even if a very extensive one—of the mechanisms of neuronal plasticity and sensomotor flexibility that are constantly updating our sensomotor representations as a result of experience. As an illustration, this review contains some new experimental results on PL and sensory flexibility in the context of adaptation to multifocal intraocular lenses.

Keywords: vision; learning; patients

1. PERCEPTUAL LEARNING

(a) *Acquiring knowledge about the world*

Animals gain knowledge about the world in two radically different ways: they are able to acquire it individually or else inherit it through their genome. The latter allows many newborn animals to immediately perform elaborate tasks, such as navigation in three dimensions by flies. The harder way is to acquire knowledge through learning. The benefit of this alternative is a much broader spectrum of possible behaviours and a faster adaptation to changing environmental conditions—an important aspect especially in long-lived animals such as humans. However, it seems that the plasticity of the human brain greatly decreases after approximately 6–10 years, at least for early sensory cortices. This early ‘window’ of plasticity, or critical period, is generally considered as sufficiently long to optimize cortical areas for the given environment of the individual—any further modifications and learning should then occur on higher levels of cortical signal processing. And indeed, it makes perfect sense not to change the early levels of processing after sufficient adaptation to the environment has taken place, since any further change in response to a specific sensomotor task on an early level of processing could possibly interfere with other tasks learned previously.

This author argues that the improvements of sensory capabilities, both early and late in life, should be considered as forms of perceptual learning (PL), which is defined as a relatively persistent improvement in the ability to detect or discriminate sensory stimuli as a result of experience.

(b) *Plasticity of sensory cortices early in life*

A number of animal studies, notably the pioneering work of Hubel & Wiesel (1977), indeed indicated that the changes of these early cortices induced by monocular deprivation or squint were more or less reversible up to a certain age of the animal, but were no longer after the critical period. In accordance with the results of these animal studies, clinical experience indicated that therapy of strabismic amblyopia, the decrease of visual acuity in a squinting but otherwise fully functional eye, was barely reversible after the age of 6–10 years. According to this widely held view, early visual cortices learn only during early life, while all later improvements are due to improved processing on later or higher cortical areas (for a relatively recent proponent of this view, see Mollon & Danilova 1996).

(c) *No plasticity of sensory cortices later in life?*

However, it seems that this theory of an ‘early’ mechanism of PL, in the sense that PL takes place almost exclusively during early development in the early sensory parts of cortex, was too narrow a view.¹ Certainly, there are reports indicating that amblyopic eyes did not improve function in adults even after the normal partner eye was lost. But in PL, there are large

* Author and address for correspondence: Bremen University, 28211 Bremen, Germany (mfahle@uni-bremen.de).

One contribution of 12 to a Theme Issue ‘Sensory learning: from neural mechanisms to rehabilitation’.

interindividual differences and recently several studies indicated that, for example, visual acuity in amblyopic eyes can be greatly improved, even in some adult patients, by suitable training (Polat *et al.* 2004; Levi & Li 2009). So maybe even the primary visual cortex has some capacity for plastic changes in adults, similar to the somatosensory cortex, as was demonstrated by the ground breaking work of Merzenich *et al.* (1988). There seems to be agreement in the literature that amblyopia is caused by a disturbance of visual processing with loss of critical information on very early stages of cortical processing. Therefore, PL would hardly be able to improve the quality of vision in adult amblyopes by counteracting this loss of information if its effects were restricted to higher cortical areas. In other words, strong improvements of vision in adult amblyopic patients would require changes in early visual cortices, maybe even involving the primary visual cortex. Hence, therapy of amblyopic patients will appear much more feasible once we can establish that the early visual cortices are plastic to a certain degree not only early in life, but also later on.

(d) Cortical plasticity and visual rehabilitation

As indicated above, the question of whether or not early sensory cortices retain plasticity in adult life is crucial for understanding and evaluating the potential of visual rehabilitation after trauma, tumours or infarcts ('stroke'). Therefore, let us first consider the reasons leading this author to the rather 'heretic' view of plasticity in early sensory cortices of adult humans, before we come back to this issue in §5.

(e) Cortical correlates of behavioural flexibility: psychophysical evidence

Behavioural results obtained, for example, by psychophysical methods are certainly not absolutely conclusive when it comes to pinpointing the exact location in the visual system of neuronal mechanisms. However, they at least allow us to restrict the realm of possible mechanisms. In this context, the specificity of improvement of some tasks for the eye used during training indicates a relatively early location of the neuronal mechanisms underlying the improvement (Karni & Sagi 1991; Poggio *et al.* 1992). Only in early stages of cortical processing are neurons selective for the eye of origin, while neurons in later stages are usually activated through both eyes. The most parsimonious explanation of eye selectivity is that PL involves, at least in some circumstances, modifications of processing in very early sensory cortices where some of the neurons are selective for the eye stimulated. It is true that in theory binocular neurons can also discriminate between the inputs to both eyes if these inputs come in different 'flavours' (Mollon & Danilova 1996); however, no evidence for differently 'flavoured' visual inputs from the two eyes has been found so far. Moreover, the input created by the same stimulus in each of the eyes will not be homogeneous, but will vary considerably due to the fact that eye tremor will shift the stimulus by several photoreceptor diameters between presentations. Hence, it is difficult to see how binocular neuronal populations will discriminate between the input classes stemming from the two

eyes, and selectivity of improvement for the eye stimulated is better compatible with the involvement of monocular neurons.

A second, weaker argument for an involvement of early cortical areas in low level or early PL is the high specificity of improvement for the orientation of simple stimuli, such as verniers (Fahle 1998; Notman *et al.* 2005; Fahle *et al.* in preparation). Training a stimulus in one orientation improves performance. Rotating the stimulus from the trained orientation by as little as 3° will then reduce the improvement roughly by half. This orientation half width of 6° is clearly narrower than the orientation bandwidth of simple cells in the primary visual cortex, and far smaller than the bandwidth in higher, or later, cortical areas. After all, later cortical areas seem to generalize from low-level stimulus attributes, such as orientation and position in the visual field, in order to allow for transfer of knowledge obtained about the objects in the world to other similar objects or for the same object at a different position. In conclusion, the high orientation specificity of improvement in most early types of PL is better compatible with an early site of improvement than with a later one. Of course, many tasks are learned on higher cortical levels, and improvement in these tasks generalizes between eyes and visual field positions.

A similar argument holds true for the high position specificity of improvement through low-level PL. A vernier discrimination task was trained at eight different positions, all at a distance of 10° from the foveola. Improvement did not transfer between these positions, i.e. observers improved at each of the positions during the 1 hour period of training, but had to start from scratch after each transition to the next of the eight positions tested (Fahle *et al.* 1995).

(f) Correlates of flexibility: theoretical considerations and top-down connections

As outlined above, the modifications of early processing should not be permanent in the sense that they change signal processing for all future stimuli—since this may decrease performance for stimuli learned earlier. For example, to detect fine detail, small receptive fields are required, while to detect shallow luminance gradients, larger fields are more suitable. On the other hand, the modifications should be long lasting in the sense that they can be activated if necessary, since this constancy distinguishes PL from adaptation processes. Therefore, the modifications of signal processing in early sensory cortices achieved through these early forms of PL should be under top-down control. The basic idea is that to absolutely optimize detection and discrimination of visual stimuli, it is essential to optimize the signal-to-noise ratio at as early a level as possible. This can be achieved by optimizing the tuning of neurons at early stages of cortical processing to the task at hand under top-down control (Herzog & Fahle 1998). This hypothesis of 'early selection' by optimally tuned cortical filters (Fahle 2004) is fully compatible with the richness of feedback connections in the brain (e.g. Bullier *et al.* 2001). For example, the lateral geniculate nucleus (LGN) receives more feedback fibres from the cortex than it sends feed-forward ones towards cortex and, in the auditory system, top-down connections go

all the way down to the receptors, i.e. the hair cells in the cochlea. Damaging these top-down connections can impair audition due to its effects on the 'cochlear amplifier' (Maison *et al.* 2002).

(g) Correlates of flexibility: top-down influences and interference

The relatively slow speed at which extremely good or even optimal performance is reached through PL and the discovery of 'interference' (see below) are two final arguments for an early site of modifications to be outlined here.

PL can continue over weeks and months, over dozens and hundreds of hours of training, asymptotically approaching a final level. Intuitively, it is clear that optimizing low-level processing by means of top-down influences—that fine-tune lower levels—is much harder than 'just' to select the optimal inputs on a higher cortical level. Hence, the first fast phase of PL—as described, for example, in vernier learning (Poggio *et al.* 1992)—may be due to improvements on higher cortical levels, while the slow phase may also involve early levels, in line with the reverse hierarchy theory (Ahissar & Hochstein 1997).

The term interference, as used above, denotes two phenomena. First, mixing several types of stimuli during training, such as different stimulus orientations, all but abolishes or at least slows down most types of early PL. This phenomenon is more easily compatible with a slow, complex top-down mechanism that requires some time and cannot cope with stimuli varying between presentations than with a mere feed-forward selection process on higher levels of cortical processing that should be able to cope with fast changing stimulus sequences. Second, improvement through low-level PL is not only highly selective for the stimulus orientation trained. It moreover decreases performance for stimulus orientations differing from the trained one—by more than approximately 15° for vernier discriminations (Fahle *et al.* in preparation). This interference is most pronounced after longer training periods (e.g. five sessions of 1 hour each) and for most pronounced changes of stimulus orientation, i.e. 90° rotations of the stimulus (Fahle & Edelman 1993).

(h) Correlates of behavioural flexibility: electrophysiological evidence

As mentioned above, psychophysical results are usually only indicative of the location of a neuronal mechanism in the brain. Therefore, electrophysiological results in animals (single cells) and humans (field potentials) as well as imaging studies (fMRI) are absolutely crucial to localize the neuronal mechanisms in the brain. Initially, the adult cat primary cortex was considered to be rather hard wired: the plasticity seen in kitten visual cortex was not found in adult ones (Hubel & Wiesel 1977). But in monkey visual cortex, Gilbert and co-workers (Gilbert & Wiesel 1992; Li *et al.* 2004) as well as other groups (Zohary *et al.* 1994; cf. also Eysel *et al.* 1998; Eysel & Schweigart 1999) found some changes of receptive field properties after modifications of visual input. Hence, even the adult visual cortex may be at least slightly plastic and therefore more similar—in this

respect—to the somatosensory cortex (see Merzenich *et al.* 1988) than hitherto thought. While the exact nature of the modifications obtained through training is not completely understood, it seems that these changes may only be activated while the animal is solving the task trained (Gilbert 1998), not in other situations (Yang & Maunsell 2004; cf. also Vogels & Orban 1994).

Field potential studies in humans point in a similar direction. An early sum-potential study found significant changes in the sum-potential distribution over the occipital cortex after the training of a vernier discrimination task, starting at a latency as short as 50 ms (Fahle & Skrandies 1994). Similar changes were obtained in a number of other training conditions in several laboratories (Skrandies *et al.* 2001; Ding *et al.* 2003; Casco *et al.* 2004). Imaging results, on the other hand, are not yet unequivocal. However, recent evidence suggests that fMRI is capable of indicating which subjects will improve through PL and which will not (Mukai *et al.* 2007). Cortical activity of 'learners' gradually decreased in several cortical areas, including early visual cortices, probably due to a sharpening of neuronal tuning.

(i) Perceptual learning, cortical plasticity and behavioural flexibility

To sum up, behavioural and electrophysiological results together provide strong arguments for the hypothesis that early cortices can change their signal processing as a result of training not only during childhood, but also later on, in adult life. Hence, the realm of PL has to be extended from childhood (i.e. early in life) towards adulthood (i.e. late in life) and, simultaneously, from late to early during cortical processing. In other words, we conjecture the existence of changes in early cortical processing later during life—eliminating the only condition for which learning and plasticity have, so far, been considered to be impossible. This conjecture opens up the possibility to address disorders of early visual processing in adults, especially in amblyopic patients (see Levi & Li 2009), but possibly also after cortical infarctions (stroke; see Daum & Widdig 2000).

2. BEYOND 'MONOLITHIC' PERCEPTUAL LEARNING: DIFFERENT LEVELS OF SENSORIMOTOR FLEXIBILITY

(a) 'Early' versus 'late' types of perceptual learning

PL often takes place on 'higher' cortical levels, not just the lower levels stressed so far (see Ahissar & Hochstein 1997). In several respects, I see similarities between PL and sensorimotor flexibility on early cortical levels, corresponding to the slow phase of PL that occurs after the fast initial improvement achieved on higher cortical levels of processing. This low-level type of PL, in my opinion, should be set apart from late forms of PL, such as discrimination between, say, different types of tissues (e.g. liver versus kidneys) or different types of wines. Early PL, as defined above, would then improve the detection of and discrimination between simple features. These features may appear close to absolute

contrast thresholds or the task may require discriminating between minuscule orientation differences of a simple stimulus. Late PL, on the other hand, according to this definition, involves the selection and evaluation of ensembles of features in order to discriminate between complex classes of features, but more dissimilar target elements. In other words, early PL in its simplest form would involve one-dimensional categories, while late PL would also involve multi-dimensional categories.

(b) *Prism adaptation as a case of sensorimotor plasticity and neuronal flexibility*

An apparently simple example for sensorimotor flexibility, achieved in a mostly subconscious and automatic way, is prism adaptation. Adaptation processes differ from PL in that they do not leave permanent changes, as for example in light adaptation. The well-known phenomenon of prism adaptation occurs when subjects wear prisms that shift the image of the outer world, for example, in a horizontal direction. As a consequence, arm movements to a visual target initially deviate in the direction dictated by the prisms. But less than 10 arm movements are usually sufficient for subjects to adapt to this deviation of visual input and to produce movements precisely towards the goal (Redding *et al.* 2005). The initial hypothesis that visual input may be shifted in the visual system in the direction opposite to the optical shift is obviously too simplistic. If it were true, adaptation should transfer to the partner arm while, in fact, it does not in many instances. In reality, prism adaptation seems to be a rather complex process of sensorimotor flexibility that occurs mostly subconsciously and automatically (while there is, unfortunately, also a cognitive component) with an after effect in the opposite direction after removal of the prisms. Over time, mechanisms of PL seem to speed up this adaptation process, allowing subjects to virtually instantaneously 'adapt' to the prisms. This is an important difference to other forms of adaptation—light adaptation cannot be speeded up by training! Given the involvement of cognitive processes and the possibility of permanent changes, the term prism 'adaptation' may hence indicate a too simplistic mechanism, and if we preserve it, we should clearly discriminate such forms of late adaptation from early forms of adaptation such as retinal light adaptation.

Wearing prisms is an extreme challenge to mechanisms that, in the author's opinion, are permanently active to fine-tune the relationship between sensory inputs and motor outputs under perpetually varying conditions of sensory stimulation (e.g. different glasses) and motor outputs (such as different weights when carrying different tools or loads). This highly flexible and adaptive neuronal network with extensive feedback/top-down connections can learn and is a far cry from the strictly feed-forward filtering bank that most people in the field (including the author) imagined two decades ago. This flexibility probably is at the heart of the superiority of the human nervous system over technical systems relying on much higher processing speeds. But this flexibility makes the endeavour to unveil the mechanisms underlying sensorimotor behaviour all the more challenging, while

giving hope to devise new means to rehabilitate patients suffering from a variety of disorders of the central nervous system.

3. A (NOT COMPLETELY) NEW VIEW ON CORTICAL FUNCTION

(a) *Difficulties to analyse in a 'plastic' system with strong feedback connections*

A few decades ago, the adult brain was considered a sequence of rather hard-wired 'boxes' that analysed, in a hierarchical and bottom-up way, the input delivered by the sense organs, with plasticity and learning reserved to specialized parts, such as the hippocampus. This author feels that the purely bottom-up view is no longer held by most researchers in the field; the view prevails that the brain indeed contains many top-down circuits and retains plasticity in many areas. Such a flexible system with plasticity present on each level of cortical processing even in adult life is, of course, the nightmare for anyone wishing to understand the nature of the mechanisms underlying the processing of this system. Probing the system might change the system, even on early levels, suggesting Heisenberg's 'uncertainty principle' ('Unschärferelation'): probing the system changes the system. However, such a highly flexible system is far more able to cope with varying task demands and with changing relations between sensory inputs and motor demands than a 'hard-wired' system would be. Take, for example, a new pair of glasses that changes retinal magnification, or grasping a tennis racket. For a trained player, his or her arm/hand just changes shape: the racket becomes part of their own body, allowing the highest precision of aim at the tennis ball. Similarly, a new pair of glasses with, say, multifocal lenses may initially cause problems in sensorimotor coordination, but these will soon fade away. In summary, we are left with a system highly flexible and adaptable even in its adult version—a great advantage for its owner even if this flexibility poses additional problems for the investigator.

(b) *The brain as a highly dynamic and flexible neuronal network that can be trained and rehabilitated*

In my opinion, prism adaptation and PL are both examples of the flexibility and plasticity present on (almost) all levels of cortical processing, even though prism adaptation initially leaves no permanent effects after the prisms are removed. It seems plausible that all forms of flexibility and plasticity induced by training may rely on similar neuronal mechanisms, namely an increase or decrease in synaptic efficiency and the formation or destruction of synapses. Given the fact that these neuronal mechanisms seem to be generally identical from aplysia to humans, why should they differ between cortical areas? Once we accept that all cortical areas retain a certain degree of plasticity even in adult life, it may be appropriate to name different types of changes in behaviour according to the main locus in the nervous system that they modify, rather than by more phenomenological classifications, as have been used so far.

(c) *Different forms and locations of brain plasticity*

It is certainly possible to discriminate between predominantly sensory versus predominantly motor plasticity, but in many cases, such as prism adaptation, the modifications will almost certainly be of a sensomotor type. Within the domain of sensory plasticity, we may want to differentiate the term 'perceptual learning', as already done above. Processes involving mainly relatively late cortical areas in the temporal and parietal cortex may be called cognitive, or late PL, while those modifying processing mostly in the occipital cortex may better be classified as 'top-down adaptations', or early PL.

These adaptive and learning processes, working mostly subconsciously, are permanently updating the signals received from different sense organs, such as the eyes, the ears, the skin and proprioceptors in the body, in order to realign the coordinate systems of different sense modalities, making sure we feel our hand to be where we see it and to see an object to be where we hear it. Prism adaptation is hence just a dramatic example of the processes that are permanently active to ensure optimal sensomotor coordination, probably involving early cortical areas.

4. PERCEPTUAL LEARNING AND SELECTIVE ATTENTION: A SPECULATION

Let us come back to the view of the adult visual system as a neuronal network with strong feedback connections (for top-down control) and with at least some plasticity left throughout the entire adult system. Thinking of it, such a system is advantageous compared to one that reserves plasticity to late processing levels. Clearly, plasticity on an early level can be a big disadvantage for an adult feed-forward system due to interference between the optimal processing types for different tasks, as mentioned above. But for a system with top-down feedback connections, it seems to be the best choice to switch, on as early a level as possible, between different (filtering) operations or processing modes to optimize the signal-to-noise ratio for different tasks.

(a) *Evidence for top-down influences on early cortical levels*

Findings abound indicating that processing on early cortical levels is modified by top-down processes commonly called 'endogenous attention'.² I conjecture here that early PL can adapt processing, within seconds in early sensory cortices, to a task learned previously. This is to say that higher cortical areas influence processing on lower levels. Hence, depending on the task, the same neurons should reply in different ways to the same stimulus. If this conjecture sounds far fetched at first, think again. Single cell recordings in animals as well as sum-potential recordings in humans and imaging studies all show that activity of neurons in early sensory cortices can be dramatically improved if a stimulus is task relevant as compared to when it is not (e.g. Kastner & Ungerleider 2000). This phenomenon is usually called selective or task-specific attention, as opposed to a general arousal or stimulus-driven

bottom-up effects of attention. All I propose is that this effect of top-down selective attention can be modified, i.e. fortified, by training (see also Ahissar & Hochstein 1997). Clearly, the effects of this type of top-down influence would depend on the control level involved, being spatially and eye selective on very early cortical levels, while less specific on 'later' levels.

(b) *Low-level perceptual learning as a modification of 'attentional' top-down influence*

This prediction will be difficult to prove in animal studies that require extensive training before the experiment proper. However, it seems that the results of sum-potential correlates of PL (modification of evoked responses on early cortical stages through training) are compatible with the view that 'selective attention' can be considered as a partly learned optimization of early neuronal signal processing under top-down control. PL achieves not merely a selection of relevant over less relevant input neurons on a later or higher processing stage.

In summary, the author does not see any reason why the nervous system should give up its ability to learn 'new tricks', in order to optimize bottom-up sensory processing under top-down control when new tasks have to be solved, at any time during life. I conjecture that the visual system not only modifies processing on a short time scale by 'adaptation' and 'attention' (see above), but that PL may optimize the effects of this top-down attention on different levels of cortical processing. This speculation is in line with the recent fMRI finding that PL modifies activations in both visual and attention-related cortical areas (Mukai *et al.* 2007). Hence, after training, one of the top-down processes (called selective attention) may modify processing on early cortical levels in a more effective way than it did before, thus improving the signal-to-noise ratio.

5. POSSIBLE APPLICATIONS OF PERCEPTUAL LEARNING IN PATIENTS

(a) *Physiological knowledge as the basis for therapy*

Therapy for various disorders of the nervous system is strongly hampered by incomplete knowledge (to say the least) of this most human of all organs. It is probably fair to say that today mankind understands the workings of all their other organs for better than they understand the brain.³ So, I devote the remainder of this chapter to some ideas and speculations, produced partly by this author's brain, regarding the workings of the human brain in general and its flexibility, which enables learning and similar phenomena both in normal observers and in patients.

(b) *Learning: faster in youngsters but still present in grown-ups*

As mentioned in the introduction, the relatively long-lived species *Homo sapiens sapiens* chose to have a comparatively small part of its sensory abilities and behavioural repertoire pre-wired at birth. This is partly due to the limitations of the information available in the genome. For example, to genetically determine for each individual retinal ganglion cell the explicit

corresponding address in the LGN and visual cortex would require an amount of storage capacity on the genome that is simply unavailable. More importantly, the openness and ability to shape both sensory and motor capabilities in interaction with the outer world make our species extremely adaptive—if somewhat unstable in some respects and prone to excess.

It has been clear for a long time that motor capabilities can be trained in adults, though with less success than in children. Most of the people starting to ski after their twentieth birthday will never be really brilliant at it and the same can be said about mastering languages, the critical period for languages ending probably even earlier. But nevertheless, some people even in their sixties or seventies do learn a new language or a new type of motor behaviour. This persistence of motor plasticity is, in fact, the cause for the broad and unanimous consensus that patients suffering from motor disturbances after strokes should receive rehabilitation treatment—which indeed often produces amazing improvements (helped by the spontaneous recovery of brain tissue). Hence, there is little doubt that motor behaviour can improve both in children and in adults; there is also little doubt that sensory abilities rapidly improve early in life. Newborns have a visual acuity of approximately 0.5/20 and a narrow visual field, but reach normal performance when entering school. However, perceptual improvement in adults was considered, and still is by many, restricted to ‘higher’ or ‘more cognitive’ (i.e. later) cortical levels in adulthood.

Above I argued that a number of facts and findings indicate that this view may be misleading. All of the cortex, including the early sensory cortices, may be plastic up to a certain point, even in adults. But our results on PL indicate vast interindividual differences in the amount of improvement between different subjects (Fahle & Henke-Fahle 1996). Hence, not every patient may improve through training, and some may not improve at all. Still, it seems now more plausible than ever to give it a try and train people, trying to compensate for functional losses (see Polat *et al.* 2004; Levi & Li 2009).

(c) *Specificity of perceptual learning as an obstacle to sensory rehabilitation*

A big obstacle in this endeavour is the fact that the earlier the site of cortical learning, the more specific the improvement seems to be for quite a number of stimulus attributes, such as its orientation and position in space. It does not help that mixed (i.e. interleaved) presentations of different stimuli further decrease the improvement, as mentioned above. A major challenge for the future will be to devise training regimes that allow generalization of improvement. First steps in this direction are, for example, the training devised by Polat *et al.* (2004) where amblyopic patients train to detect Gabor patches and later generalize to discriminate the letters of a low-contrast acuity chart (see also Kaymak *et al.* 2008).

(d) *Perceptual learning after implantation of multifocal intraocular lenses*

In a pilot study, we trained patients in an orientation discrimination task who had received multifocal rather

than the usual monofocal intraocular lenses during cataract surgery. The multifocal, or usually bifocal, lenses have two focal lengths, one for close up (approx. 50 cm) and the other for around infinity. These patients’ retina always receives two images of each object, at least one of them blurred. Especially shortly after the operation, the halos produced by the out-of-focus image disturb vision both subjectively and as measured with optotypes. Five training sessions with an orientation discrimination task significantly improved letter acuity in the trained eye for near vision in 10 patients, a surprising but clear sign of generalization of improvement through training (Kaymak *et al.* 2008). To sum up, there seems to be hope to devise training tasks that generalize—even if the training employs stimuli close to threshold and that are, according to the reverse hierarchy theory, learned on early cortical levels.

(e) *Outlook: consequences for visual rehabilitation*

In conclusion, both psychophysical and electrophysiological results indicate that the sensory cortices even of adults retain a certain degree of plasticity that enables significant flexibility of sensorimotor behaviour. This flexibility shows up not only in PL, but in a number of ‘low-level’ tasks, such as the so-called prism adaptation. Together, these findings profoundly changed our view of our brains. Brains seem to be neuronal networks with strong top-down connections and a much higher degree of plasticity throughout the entire system than hitherto thought. As a speculation, this review links early PL with a process known as selective attention, conjecturing that early PL may increase and fine-tune the effects that attention has on the processing in early cortical areas. Extending the plasticity of cortical function to sensory cortices certainly opens up the possibility of compensating for deficits in cortical processing, may they be due to developmental problems, neuronal degenerations such as dementia or through localized destructions, such as in strokes. This volume shows some promising ways to achieve neuronal rehabilitation, based on our improved knowledge of cortical function.

Supported by DFG grant FA119/17-1.

ENDNOTES

¹To clearly distinguish between the two meanings of early in the context of this chapter, I will refer to improvements early during life from here on as ‘childhood learning’ and to those later in life as ‘adult learning’, thus retaining the terms early and late for different stages—and areas—of cortical processing.

²Attention in this context is defined as a process in the brain that selectively improves the representation of a stimulus, often simultaneously causing deterioration in the representations of other stimuli.

³There are people who even doubt that it is possible for one organ (the brain) to understand itself. But this is sophism, in my opinion, and the first computers designing new computers will hopefully silence these sceptics once and for all.

REFERENCES

- Ahissar, M. & Hochstein, S. 1997 Task difficulty and learning specificity: reverse hierarchies in sensory processing and perceptual learning. *Nature* **387**, 401–406. (doi:10.1038/387401a0)

- Bullier, J., Hupé, J.-M., James, A. C. & Girard, P. 2001 The role of feedback connections in shaping the responses of visual cortical neurons. *Prog. Brain Res.* **134**, 193–204. (doi:10.1016/s0079-6123(01)34014-1)
- Casco, C., Campana, G., Grieco, A. & Fuggetta, G. 2004 Perceptual learning modulates electrophysiological and psychophysical response to visual texture segmentation in humans. *Neurosci. Lett.* **371**, 18–23. (doi:10.1016/j.neulet.2004.08.005)
- Daum, I. & Widdig, W. (eds) 2000 *Aktuelle Aspekte der Neurorehabilitation*. Lengerich, Germany: Pabst.
- Ding, Y., Song, Y., Fan, S., Qu, Z. & Chen, L. 2003 Specificity and generalization of visual perceptual learning in humans: an event-related potential study. *Neuroreport* **14**, 587–590. (doi:10.1097/00001756-200303240-00012)
- Eysel, U. T. & Schweigart, G. 1999 Reorganization of receptive fields at the border of chronic visual cortical lesions. *Cereb. Cortex* **9**, 101–109. (doi:10.1093/cercor/9.2.101)
- Eysel, U. T., Eyding, D. & Schweigart, G. 1998 Repetitive optical stimulation elicits fast receptive field changes in mature visual cortex. *Neuroreport* **9**, 949–954. (doi:10.1097/00001756-199803300-00034)
- Fahle, M. 1998 Orientation specificity of perceptual learning. *Invest. Ophthalmol. Visual Sci.* **39**, 912.
- Fahle, M. 2004 Perceptual learning: a case for early selection. *J. Vis.* **4**, 879–890. (doi:10.1167/4.10.4)
- Fahle, M. & Edelman, S. 1993 Long-term learning in vernier acuity: effects of stimulus orientation, range and of feedback. *Vis. Res.* **33**, 397–412. (doi:10.1016/0042-6989(93)90094-D)
- Fahle, M. & Henke-Fahle, S. 1996 Inter-observer variance in perceptual performance and learning. *Invest. Ophthalmol. Visual Sci.* **37**, 869–877.
- Fahle, M. & Skrandies, W. 1994 An electrophysiological correlate of perceptual learning in humans. *Germ. J. Ophthalmol.* **3**, 427–432.
- Fahle, M., Edelman, S. & Poggio, T. 1995 Fast perceptual learning in hyperacuity. *Vis. Res.* **35**, 3003–3013. (doi:10.1016/0042-6989(95)00044-Z)
- Fahle, M., Spang, K. & Herzog, M. In preparation. On the orientation specificity of perceptual learning.
- Gilbert, C. D. 1998 Adult cortical plasticity. *Physiol. Rev.* **78**, 467–485.
- Gilbert, C. D. & Wiesel, T. N. 1992 Receptive field dynamics in adult primary visual cortex. *Nature* **356**, 150–152. (doi:10.1038/356150a0)
- Herzog, M. & Fahle, M. 1998 Modelling perceptual learning: difficulties and how they can be overcome. *Biol. Cybern.* **78**, 107–117. (doi:10.1007/s004220050418)
- Hubel, D. H. & Wiesel, T. N. 1977 Functional architecture of macaque monkey visual cortex. *Proc. R. Soc. B* **198**, 1–59. (doi:10.1098/rspb.1977.0085)
- Karni, A. & Sagi, D. 1991 Where practice makes perfect in texture discrimination: evidence for primary visual cortex plasticity. *Proc. Natl Acad. Sci. USA* **88**, 4966–4970. (doi:10.1073/pnas.88.11.4966)
- Kastner, S. & Ungerleider, L. G. 2000 Mechanisms of visual attention in the human cortex. *Annu. Rev. Neurosci.* **2**, 315–341.
- Kaymak, H., Fahle, M., Ott, G. & Mester, U. 2008 Intraindividual comparison of the effect of training on visual performance with ReSTOR and Tecnis diffractive multifocal IOLs. *J. Refract. Surg. Mar.* **24**, 287–293.
- Levi, D. M. & Li, R. W. 2009 Improving the performance of the amblyopic visual system. *Phil. Trans. R. Soc. B* **364**, 399–407. (doi:10.1098/rstb.2008.0203)
- Li, W., Piéch, V. & Gilbert, C. D. 2004 Perceptual learning and top-down influences in primary visual cortex. *Nat. Neurosci.* **7**, 651–657. (doi:10.1038/nn1255)
- Maison, S. F., Luebke, A. E., Liberman, M. C. & Zuo, J. 2002 Efferent protection from acoustic injury is mediated by alpha 9 nicotinic acetylcholine receptors on outer hair cells. *J. Neurosci.* **22**, 10 838–10 846.
- Merzenich, M. M., Recanzone, G., Jenkins, W. M., Allard, T. T. & Nudo, R. J. 1988 Cortical representational plasticity. In *Neurobiology of neocortex* (eds P. Rakic & W. Singer), pp. 41–67. New York, NY: Wiley.
- Mollon, J. D. & Danilova, M. V. 1996 Three remarks on perceptual learning. *Spat. Vis.* **10**, 51–58. (doi:10.1163/156856896X00051)
- Mukai, I., Kim, D., Fukunaga, M., Japee, S., Marett, S. & Ungerleider, L. G. 2007 Activations in visual and attention-related areas predict and correlate with the degree of plasticity. *J. Neurosci.* **27**, 11 401–11 411. (doi:10.1523/JNEUROSCI.3002-07.2007)
- Notman, L. A., Sowden, P. T. & Ozgen, E. 2005 The nature of learned categorical perception effects: a psychophysical approach. *Cognition* **95**, B1–B14. (doi:10.1016/j.cognition.2004.07.002)
- Poggio, T., Fahle, M. & Edelman, S. 1992 Fast perceptual learning in visual hyperacuity. *Science* **256**, 1018–1021. (doi:10.1126/science.1589770)
- Polat, U., Ma-Naim, T., Belkin, M. & Sagi, D. 2004 Improving vision in adult amblyopia by perceptual learning. *Proc. Natl Acad. Sci. USA* **101**, 6692–6697. (doi:10.1073/pnas.0401200101)
- Redding, G. M., Rossetti, Y. & Wallace, B. 2005 Applications of prism adaptation: a tutorial in theory and method. *Neurosci. Biobehav. Rev.* **29**, 431–444. (doi:10.1016/j.neubiorev.2004.12.004)
- Skrandies, W., Jedynek, A. & Fahle, M. 2001 Perceptual learning: psychophysical thresholds and electrical brain topography. *Int. J. Psychophysiol.* **41**, 119–129. (doi:10.1016/S0167-8760(00)00177-X)
- Vogels, R. & Orban, G. A. 1994 Does practice in orientation discrimination lead to changes in the response properties of macaque inferior temporal neurons? *Eur. J. Neurosci.* **6**, 1680–1690. (doi:10.1111/j.1460-9568.1994.tb00560.x)
- Yang, T. & Maunsell, T. H. 2004 The effect of perceptual learning on neuronal responses in monkey visual area. *J. Neurosci.* **24**, 1617–1626. (doi:10.1523/JNEUROSCI.4442-03.2004)
- Zohary, E., Celebrini, S., Britten, K. H. & Newsome, W. T. 1994 Neuronal plasticity that underlies improvement in perceptual performance. *Science* **263**, 1289–1292. (doi:10.1126/science.8122114)