

Sleeper effects

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Abstract

Early experience preserves and refines many capabilities that emerge prenatally. Here we describe another role that it plays – establishing the neural substrate for capabilities that emerge at a much later point in development. The evidence comes from sleeper effects: permanent deficits when early experience was absent in capabilities that normally emerge long after birth. We provide evidence of sleeper effects for three aspects of vision, based on our research with children who were deprived of early visual input by congenital cataracts: contrast sensitivity for mid and high spatial frequencies, holistic face processing, and the ability to recognize the identity of faces based on small differences in the spacing among facial features.

Introduction

Early experience is necessary to preserve and refine many capabilities, often through the interaction of innate architectural constraints with an expectable human environment. Clear examples come from animal studies of visual development: patterned visual input is necessary to preserve ocular dominance columns that are formed prenatally, at least in monkeys, and to allow the refinement of orientation sensitivity (Crawford, Pesch, von Noorden, Harwerth & Smith, 1991). Here we illustrate another role that early experience can play: it can set up or preserve the neural substrate for a capability that will emerge at a much later point in development. When the early experience is lacking, the capability fails to develop normally many years later. We have seen that pattern in children who were born with bilateral dense cataracts that caused visual deprivation during infancy. Despite treatment within months of birth, some visual capabilities fail to develop during later childhood. After describing the patient cohort, we will give three examples of such sleeper effects: sensitivity to mid and high spatial frequencies, holistic face processing, and sensitivity to facial identity based on the spacing of internal features. We end with two hypotheses about the origins of sleeper effects and their implications for understanding normal development.

Children in the patient cohort were born with dense, central cataracts in both eyes that blocked all patterned input to the retina. The cataractous lenses were removed during infancy and the eyes given compensatory contact lenses to focus visual input. The child's age at the end of visual deprivation varied from 1 month to more than a year. We have followed this cohort longitudinally from the time of treatment and compared them to age-matched groups of visually normal children. Examination of the final outcome indicates that some visual capabilities recover completely: sensitivity to low spatial frequencies (wide stripes at low contrast), sensitivity to high temporal frequencies (high rates of flicker), face detection, and recognition of facial identity based on the shape of internal features or of the external contour (Elleberg, Lewis, Maurer, Lui & Brent, 1999b; Le Grand, Mondloch, Maurer & Brent, 2001, 2003, 2004; Maurer, Elleberg & Lewis, 2006; Mondloch, Le Grand & Maurer, 2003). However, there are severe, permanent deficits in sensitivity to mid and high spatial frequencies (medium and narrow stripes), in holistic face processing, and in recognition of facial identity based on the spacing of features, even when the visual deprivation ended in the first few months of life. In the visually normal child, each of these capabilities emerges postnatally and is not adult-like until long after infancy. Thus, visual deprivation during infancy prevents the later development of some aspects of normal

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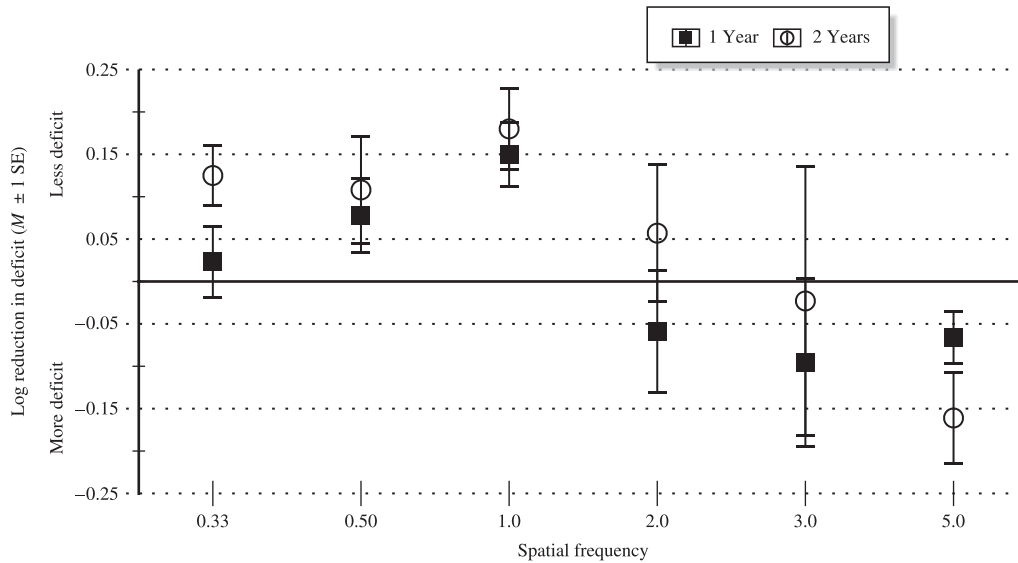


Figure 1 Reduction in patients' deficit in contrast sensitivity when re-tested 1 or 2 years after the initial assessment. The first test was between age 4 and 7 years. The graph shows how the patients' deficit, compared to visually normal controls, changed when they were re-tested 1 and 2 years later. For low spatial frequencies (wide stripes: up to 1.0 cycle per degree), patients' sensitivity improved more than that of controls, eliminating all or most of their deficit. For mid spatial frequencies (3–5 cycles per degree), there was improvement in the control group but not in the patients, so that patients' deficit increased. For high spatial frequencies (10–20 cycles per degree), patients were unable to see the stripes at any test point. Reprinted from Maurer, Ellemberg & Lewis (2006, Figure 4).

vision. This is what we refer to as a sleeper effect. We will give examples from contrast sensitivity, holistic face processing, and the recognition of facial identity.

Contrast sensitivity

Newborns can see but their acuity and contrast sensitivity are poor: acuity is at least 40 times worse and sensitivity to contrast at least 50 times worse than they are in adults (Atkinson, Braddick & Moar, 1977; Banks & Salapatek, 1978; Brown & Yamamoto, 1986; Courage & Adams, 1990; van Hof-van Duin & Mohn, 1986; reviewed in Maurer & Lewis, 2001a, 2001b). There is no response at all to stripes narrower than 1 cycle per degree (0.5 cm wide when viewed from 57 cm). Over the first 6 months, there is five-fold improvement in acuity and some improvement in contrast sensitivity so that the infant responds to mid spatial frequencies of high contrast (up to 5 cycles per degree). Sensitivity to high spatial frequencies (narrow stripes) emerges gradually after 1 year of age. Even at age 4, the child's contrast sensitivity is 0.5 log units lower than that of adults for mid spatial frequencies and the highest spatial frequency that is visible is lower than in adults (Ellemberg, Lewis, Liu & Maurer, 1999a). Acuity is not adult-like until 4 to 6 years of age and contrast sensitivity not until 7 years of age (Ellemberg

et al., 1999a; Mayer & Dobson, 1982; but see Gwiazda, Bauer, Thorn & Held, 1997).

Children treated for bilateral congenital cataracts eventually achieve normal contrast sensitivity at low spatial frequencies. Immediately after treatment, their vision is like that of newborns (Maurer, Lewis, Brent & Levin, 1999), but they start to improve faster-than-normal so that they match the (relatively poor) acuity of a visually normal 12-month-old by the first birthday (Lewis, Maurer & Brent, 1995) and they overcome the initial deficit in contrast sensitivity for low spatial frequencies after age 5 (Maurer *et al.*, 2006; Ellemberg *et al.*, 1999b; see Figure 1). Evidently, the innate architectural constraints combined with delayed visual input are sufficient to induce normal contrast sensitivity for low spatial frequencies, the range that is visible at high contrasts at birth.

Patients' developmental trajectory is quite different for mid and high spatial frequencies, which develop much more slowly in visually normal children (Ellemberg *et al.*, 1999a). At age 5 to 6 years, patients treated for bilateral congenital cataracts fail to see higher spatial frequencies even at maximum contrast. They can see mid spatial frequencies but their sensitivity is poor: they require about 30 times more contrast than normal to detect stripes of 5 cycles per degree (Maurer *et al.*, 2006). The contrast sensitivity of visually normal children increases two-fold for mid and high spatial frequencies between 5 and

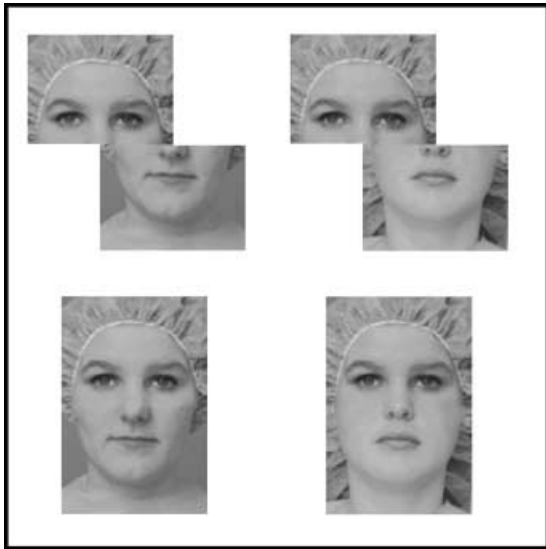


Figure 2 Test stimuli for the composite face effect. On ‘same’ trials, the top halves of the two sequential faces are the same but they are combined with different bottom halves. The subjects’ task is to indicate that the tops are the same. When the halves are aligned in upright faces, visually normal adults find the task difficult on same trials because holistic processing creates the impression of two different faces. When the halves are misaligned to break holistic processing, the task is much easier. Reprinted from Le Grand, Mondloch, Maurer & Brent (2004, Figure 1, left panel).

7 years of age whereas patients’ contrast sensitivity in this range of spatial frequencies does not change after 5 years of age (Elleberg *et al.*, 1999a; Maurer *et al.*, 2006; reviewed in Maurer & Lewis, 2001a, 2001b). Thus, patients’ deficits become larger and larger (see 5.0 cycles/degree in Figure 1). This is an example of a sleeper effect: visual deprivation in the first few months of life prevents the development of sensitivity to mid and high spatial frequencies – sensitivity that normally emerges later in infancy and childhood and that is refined by visual input during the school years, leaving the typical patient with the contrast sensitivity of a visually normal toddler (Gwiazda *et al.*, 1997).

Holistic face processing

Unlike other objects, adults process faces holistically: they integrate the parts into a whole or Gestalt-like representation, thereby reducing the accessibility of information about individual features (reviewed in Maurer, Le Grand & Mondloch, 2002). A classic measure of holistic processing is the *composite face effect*. When adults are asked to recognize the top half of a face (as

belonging to a celebrity or being the same as the top half of the face that preceded it), they have difficulty if the top half has been combined with the bottom half of a different face (Young, Hellawell & Hay, 1987; Hole, 1994). Presumably, holistic processing binds the two halves together, creating a novel face in which it is difficult to selectively attend to the top (see Figure 2). Performance improves if the top and bottom halves are misaligned, presumably because misalignment disrupts holistic processing. Similarly, adults recognize that a feature belongs to a particular individual (e.g. Larry’s nose) more easily if it is presented in the context of the rest of the face (within Larry’s face) than if it is presented in isolation, a phenomenon called the *whole/part advantage* (Tanaka & Farah, 1993). These findings demonstrate that the features of upright faces are not represented individually, but rather form a holistic representation that is so well integrated that it is difficult to parse the face into isolated features.

Infants have not been tested directly for the composite face effect or whole/part advantage. However, young infants process faces and other objects in a piecemeal fashion (reviewed in Cashon & Cohen, 2004). For example, 3-month-olds treat a recombined face comprising the internal features of one familiar face with the external contour of another familiar face as a familiar face and not until 4 months of age do they treat the recombined face as novel (Cashon & Cohen, 2003, 2004). By 4 years of age (youngest age tested), children show the whole/part advantage, with no significant change in the size of the whole advantage between 4 years of age and adulthood (Pellicano & Rhodes, 2003). By age 6 (youngest age tested), they show the composite face effect for both familiar and unfamiliar faces and the magnitude of the effect is adult-like (Carey & Diamond, 1994; Mondloch, Pathman, Maurer, Le Grand & de Schonen, in press).

Holistic processing appears to be tuned by postnatal experience with human faces: neither the composite face effect nor the whole/part advantage occurs for inverted faces. The whole/part advantage does not occur for drawings of houses (Tanaka & Farah, 1993) and the composite face effect does not occur for unfamiliar objects like greebles with which the viewer has not been trained (Gauthier & Tarr, 2002). Both effects are stronger for own-race than other-race faces, unless the subject has been living for more than a year among individuals of the other race (Michel, Caldara & Rossion, in press; Michel, Rossion, Han, Chung & Caldara, 2006; Tanaka, Kiefer & Bukach, 2004).

Our studies of patients treated for bilateral congenital cataract indicate that early visual experience is necessary if holistic processing is to develop later in life. When tested for the composite face effect at a mean age of

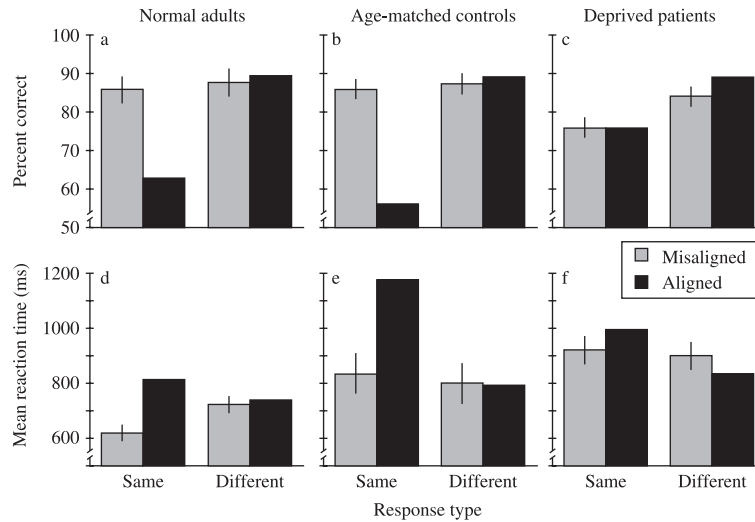


Figure 3 Results for the composite face task for patients treated for bilateral congenital cataract and age-matched controls. On the critical probe trials (same/aligned), the control group is less accurate and has longer reaction times compared to both the patient group and their own performance when the holistic interference from the irrelevant bottom half is reduced by misalignment (same/misaligned). Patients’ superior performance on same/aligned trials and their identical performance on same trials for the aligned and misaligned blocks both provide evidence that the patients do not process faces holistically. Reprinted from Le Grand, Mondloch, Maurer & Brent (2004, Figure 2).

15 years (range 9–23 years), patients showed no evidence of holistic processing and in fact performed better than controls on the critical condition where holistic processing interferes with accuracy: patients were more accurate and faster than controls in seeing that two top halves were the same when the top halves were aligned with two different bottom halves and, unlike controls, did no better when the halves were misaligned to break holistic processing (Le Grand, Mondloch, Maurer & Brent, 2004). By this superior performance, the patients demonstrated that they do not process faces in a normal holistic manner. This deficit was evident even when the deprivation had ended by 3 months of age, before the age at which visually normal infants show the first signs of holistic processing. Hence this is another example of a sleeper effect: early visual experience is necessary to set up (or maintain) the neural substrate that leads to the later emergence of holistic processing of faces and its later tuning by the details of the individual’s experience.

Recognition of facial identity based on spacing of features

Adults use three types of information to individuate upright faces: the shape of the external contour (e.g. chin), the shape of individual internal features (e.g. the eyes, eyebrows, and mouth), and the spacing of the internal features (e.g. distance between the eyes) (reviewed in

Mondloch, Le Grand & Maurer, 2002; see Figure 4). The last cue engages a type of configural processing called sensitivity to second-order relations (Diamond & Carey, 1986) that adults can use effectively only with upright faces (e.g. Freire, Lee & Symons, 2000; Mondloch *et al.*, 2002) and only when low spatial frequencies are present in the image (Goffaux, Hault, Michel, Vuong & Rossion, 2005). Processing of featural spacing may allow adults to recognize a face’s identity despite changes in the shape of individual features as the head is turned or the individual conveys different emotional expressions. Hence, it is critical to adults’ expertise in recognizing facial identity in upright faces.

Habituation procedures have shown that the ability to discriminate very large spacing changes that fall outside natural limits emerges between 3 and 5 months of age (Bhatt, Bertin, Hayden & Reed, 2005; Bertin & Bhatt, 2004), but even at 7 months babies fail to discriminate spacing differences that stay within natural limits (see Figure 4, Panel C; Le Grand, Maurer & Mondloch, 2004). At 4 years of age, children detect changes in the internal features of children’s faces they learned to recognize from a storybook and in a picture of their own face, but they fail to notice differences in the spacing of features that stay within natural limits (Mondloch, Leis & Maurer, 2006; see also Freire *et al.*, 2000). Six-year-olds are above chance at detecting changes in the spacing of features, but even 14-year-olds make more errors than adults (see Figure 4, Panel C; Mondloch *et al.*, 2002, 2003).



Figure 4 The stimulus sets used to test sensitivity to differences among faces in the shape of the eyes and mouth (set A), the shape of the external contour (set B), and the spacing of the internal features (set C). 'Jane' is shown as the left-most face in each panel, along with her sisters differing along one of the three dimensions. For the tests, stimuli were presented almost life size. Patients treated for bilateral congenital cataract have a deficit only when asked to discriminate faces in the spacing set (C). Reprinted from Le Grand, Mondloch, Maurer & Brent (2003, Figure 1).

In contrast, detection of featural changes is nearly adult-like by 6 years of age (see Figure 4, Panels A and B; Mondloch *et al.*, 2002). Thus, use of second-order relations as a cue to facial identity emerges postnatally and continues to improve into adolescence. Like holistic processing, sensitivity to second-order relations is tuned by experience with faces after birth: in adults, it is better for upright than inverted faces (Collishaw & Hole, 2000; Freire *et al.*, 2000; Mondloch *et al.*, 2002; Rhodes,

Hayward & Winkler, 2006), better for human than for monkey faces (Mondloch, Maurer & Ahola, in press), and better for own-race than other-race faces (Rhodes *et al.*, 2006).

Our studies of children treated for bilateral congenital cataract indicate that early visual deprivation prevents the later development of normal sensitivity to second-order relations. Patients were tested at a mean age of 14 years (range 9–21 years) and their performance was

compared to age-matched controls. When asked to make same/different judgments about pairs of faces, patients performed normally when the faces differed only in the external contour or only in the shape of the eyes and mouth. However, they were severely impaired, although above chance, when the two faces differed only in the spacing between the eyes and the spacing between the eyes and mouth (Le Grand *et al.*, 2001; Mondloch *et al.*, 2003). The deficit was evident even when deprivation had been limited to the first 2–3 months of life. This is a third example of a sleeper effect: visual input during the first few months of life – before any sign of sensitivity to second-order relations – is necessary if sensitivity to second-order relations is to emerge later and be fine-tuned by the individual's experience with faces.

Developmental mechanisms

Despite early visual deprivation, children treated for cataract eventually develop normal contrast sensitivity for low spatial frequencies and high temporal frequencies and normal ability to recognize facial identity based on the shape of external contour or internal features – all of which are capabilities that are already present at birth in rudimentary form. Other aspects of contrast sensitivity and face processing show sleeper effects – permanent deficits in capabilities that emerge postnatally in the visually normal child. In this paper we gave three examples: contrast sensitivity for mid and high spatial frequencies, holistic face processing, and recognition of facial identity based on the spacing of features, or second-order relations. Here we consider two developmental mechanisms that may explain the sleeper effects.

Loss of the optimal neural architecture

One possibility is that each of the affected visual capabilities is mediated by a neural network consisting of interconnected neurons with optimal characteristics for that type of processing. For example, holistic face processing and sensitivity to the spacing of facial features both require the integration of information over large parts of space and hence require neurons with large receptive fields that receive inputs from neurons that code more detailed information in smaller receptive fields. Learning the identity of an individual is facilitated by simultaneous input from a number of modalities (visual features and their spacing, voice cues, distinctive patterns of movement) and hence favours a network with multi-modal inputs. Seeing high spatial frequencies, in contrast, requires neurons with small receptive fields that can sharpen contours

via opponent excitatory and inhibitory regions. Sleeper effects may arise because early visual input is necessary to preserve or establish the optimal neuronal architecture for each task. In the absence of visual input, the hardware and/or its connections may be eliminated or may be recruited, through Hebbian competition, for another ability, much as the visual cortex becomes specialized for hearing and touch in the congenitally blind (reviewed in Maurer, Lewis & Mondloch, 2005). By this account, the absence of the optimal neural architecture prevents the patients treated for cataract from developing the normal level of skill later in life. They may bump into limits in the remaining architecture and/or use alternative pathways for vision that have inherent limits in what they can mediate. In the visually normal child, then, early visual input reserves the architecture for vision ('buys the lot') so that it can be used for a later specialized function ('building the house').

Adverse effects of altered timing and/or sequence of inputs

An alternative – and not mutually exclusive – possibility is that early visual deprivation leads to sleeper effects by altering the normal timing or sequence of inputs. For example, in the visually normal child, the only effective input from faces for the first several months of life is low-pass. Thus, the initial tuning of cortical neurons to faces is to their low spatial frequency components that define the external contour and the basic layout of internal features. There is no effective input at this point from mid and high spatial frequencies that specify the details of features. Such a system is optimal for responding to the configurational properties of faces but not to their featural details and may develop in the right hemisphere because of its relatively greater maturity early in development (de Schonen & Mathivet, 1989). In contrast to this normal case, the patient treated for bilateral congenital cataract initially receives no patterned visual input and then has acuity that improves faster than normal: within one hour of receiving the first visual input patients' visual acuity improves from that of a normal newborn to that of a normal 6-week-old baby (Maurer *et al.*, 1999) and over the next month it continues to improve faster than normal. This rapid recovery of acuity has the side effect of eliminating a long period limited to low spatial frequency input from faces. It may prevent the normal specialization of the right hemisphere for holistic face processing and the processing of second-order relations (see Le Grand *et al.*, 2003, for corroborating evidence of the importance of input to the right hemisphere). Similarly, improvements in sensitivity to mid and high spatial

frequencies may depend on earlier improvements in sensitivity to low spatial frequencies – and hence fail to occur if sensitivity to low spatial frequencies takes 7–8 years to normalize (or nearly normalize) as we found in the bilateral patients. Alterations in the normal sequence of inputs across modalities may also contribute to the sleeper effects seen in face processing because the child learns to recognize mom well from odor and voice cues during the period of deprivation and that earlier learning prevents normal visual learning after treatment for the cataracts, much as precocious visual experience impedes auditory imprinting in quails (Lickliter, 2000) and first-language learning can impede second-language learning, at least in neural networks (Thomas & Johnson, 2006).

Implications for normal development

The sleeper effects described here indicate that patterned visual input immediately after birth plays a vital role in the construction and/or preservation of the neural architecture that will later mediate sensitivity to fine detail and expert face processing. Specifically, the low spatial frequencies that newborns can see set up a system, probably in the right hemisphere, for later learning about configural properties of faces and a system, probably in both hemispheres, for later development of fine acuity and sensitivity to mid spatial frequencies of low contrast. Both systems are refined by later visual experience – but only if their basic architecture was set up (or maintained) by stimulating the crude vision of the newborn. When the timing of that crude early visual experience is delayed until cataracts are removed, some visual capabilities will show sleeper effects: they will fail to emerge at a later point in childhood, perhaps because the requisite neural architecture is no longer available.

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