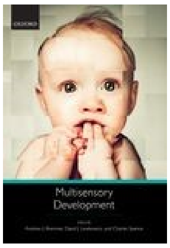

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CHAPTER

10 Infant synaesthesia: New insights into the development of multisensory perception

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Abstract

Synaesthesia is a neurological phenomenon that often involves crossmodal or cross-dimensional perceptions which are not related to environmental stimuli. Stimulation of one sense, such as hearing, triggers the normal perception of a specific sound, but also an additional perception, often in another sense, such as a specific colour. This chapter summarizes the evidence suggesting that synaesthesia is a remnant of a normal developmental process involving an initial proliferation of synaptic connections, including connections linking cortical areas that will later become specialized for unisensory processing. An argument is put forward that crossmodal and cross-dimensional associations commonly manifested in synaesthetic adults provide clues about cortical connections in early childhood that may influence perception in the typical non-synaesthetic child. Behavioural evidence from children is provided to support this point of view. This chapter also argues that remnants of the original connections are present even in non-synaesthetic adults, in whom their influence is manifested not in conscious perception, but in implicit crossmodal associations in perception.

Keywords: synaesthesia, multisensory development, perceptual development, neuroimaging, developmental neuroscience, newborns

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10.1 Synaesthesia

Synaesthesia is a neurological phenomenon that involves crossmodal or cross-dimensional perceptions that are not related to environmental stimuli. Stimulation of one sense, such as hearing, triggers the normal perception of a specific sound, but also an additional perception in another sense, such as a specific colour. Most of the 63 forms of synaesthesia identified to date (Day 2011) are multisensory (e.g. in 'coloured hearing', stimulation of one sense evokes an additional perception in a different sense). However, one common form, called 'coloured-grapheme synaesthesia', is unisensory and involves perceiving black letters and digits in colour. These extra perceptions are highly specific within each individual synaesthete, but vary to a large extent across synaesthetes. For example, among synaesthetes with coloured hearing, middle C played on the piano may induce fire-engine red for one synaesthete and chartreuse for another, while D sharp above middle C induces lavender for the first and vermilion for the second. Individuals often report more than one form of synaesthesia and, regardless of its type, the synaesthetic perceptions are consistent over time. These unusual crossmodal perceptions are automatic and involuntary, and synaesthetes report having had them 'all their lives'. In 'projector' synaesthetes, the synaesthetic perceptions are experienced as superimposed onto real-world stimuli, while in 'associator' synaesthetes, synaesthetic perceptions are experienced as internal, unavoidable associations in the 'mind's eye' (Dixon *et al.* 2004).

In this chapter, we will summarize evidence that synaesthesia is a remnant of a normal developmental process involving an initial proliferation of synaptic connections, including connections linking cortical areas that will later become specialized for unisensory processing. Postnatal experience refines those connections by strengthening those that match the child's environment and largely eliminating the rest. In synaesthesia, more of these initial connections appear to remain, with the ability to influence conscious perception. Therefore, we will argue that crossmodal and cross-dimensional associations commonly manifested in synaesthetic adults provide clues about cortical connections in early childhood that may influence perception in the typical non-synaesthetic child. We will provide behavioural evidence from children supporting this viewpoint. We will also argue that remnants of the original connections are present even in non-synaesthetic adults, in whom their influence is manifested not in conscious perception, but in implicit crossmodal associations in perception.

In the first section of this chapter, we will review evidence on the nature of synaesthetic perception and its neural basis. In the middle section, we summarize the evidence on the developmental origins of synaesthesia. In the final section, we will derive hypotheses from research on synaesthesia for understanding the perception of typical non-synaesthetic children and present evidence verifying some of those hypotheses. This perspective provides new insights into the development of perception and even language.

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10.2 Perceptual manifestations

Synaesthetic experiences can occur across different senses (e.g. ‘coloured hearing’) or within the same sense (e.g. ‘coloured graphemes’). It is difficult to estimate the prevalence of synaesthesia, as some individuals with the condition are not aware that their perceptual experiences are atypical, while others keep their synaesthetic experiences private to avoid being stigmatized (Rich *et al.* 2005). Earlier estimates of the prevalence of synaesthesia ranged from 1 in about 200 (Ramachandran and Hubbard 2001) to 1 in 25,000–100,000 (Cytowic 1997). However, these estimates are based on the frequency with which adults refer themselves to researchers studying synaesthesia, and, as such, likely underestimate the true incidence. Studies of the general population of university students indicate a much higher prevalence. Two experiments investigated the prevalence of sequence-form synaesthesia, in which ordinal sequences like numbers, days of the week, or months of the year are perceived in specific spatial locations (Galton 1881), in samples of 50 (Mann *et al.* 2009) and 500 university students (Sagiv *et al.* 2006b). Approximately one-quarter of the students reported at least one manifestation of sequence-form synaesthesia, and those who reported these associations were faster at behavioural tasks requiring mental manipulations of the sequence (e.g. name every second month in reverse chronological order; Mann *et al.* 2009). Another study investigated the prevalence of other forms of synaesthesia (excluding sequence-form synaesthesia) in a large sample of 500 university students. The students were asked to give details of any synaesthetic experiences corresponding to a list of possible inducers on an original test and a surprise retest 6 months later (Simner *et al.* 2006). Their consistency was compared to that of adults reporting no synaesthesia, who also made crossmodal associations to the same items during two sessions just 2 weeks apart. Among the 500 participants, 4.4% reported at least one type of synaesthesia, which was verified by its greater consistency in the synaesthetic group than that shown by the control group. Most forms involved colour as the extra elicited perception, with coloured-grapheme synaesthesia reported by 45% of those indicating at least one form of synaesthesia. A similar prevalence for colour-grampheme synaesthesia (1.1% of the general population) was found in a survey of 1190 individuals recruited at a science centre (Simner *et al.* 2006) and in a study of 615 children aged 6–8 years old (1.3%; Simner *et al.* 2009a).

The possibility of a female bias in synaesthesia has been raised repeatedly in the literature, with estimates of a female:male ratio as high as 6:1 (Baron-Cohen *et al.* 1996; Rich *et al.* 2005). However, this purported female bias likely reflects a greater reluctance of men than women with synaesthesia to identify themselves by contacting researchers. The two aforementioned studies performed with university students and science-centre patrons both suggest that all forms of synaesthesia occur equally often in men and women, including the two most common types of the condition (sequence-form and coloured-grapheme synaesthesia; Sagiv *et al.* 2006a; Simner *et al.* 2006).

Galton (1881) was the first to describe the possibility of a familial basis for synaesthesia when he observed that many of the sequence-form synaesthetes he encountered had close relatives with similar perceptual experiences. Subsequent investigations have revealed that 33–44% of synaesthetes recruited by self-referral report at least one other family member with synaesthesia (Barnett *et al.* 2008; Baron-Cohen *et al.* 1996; Ward and Simner 2005), although often not of the same type ↳ and never with exactly the same synaesthetic perceptions. Family-tree analyses have revealed no case of father–son transmission, but two cases of monozygotic twins (one pair of each sex) in which one twin is synaesthetic and the other is not (Smilek *et al.* 2002; Smilek *et al.* 2005). These patterns in twins indicate that synaesthesia is not caused by a single dominant gene. Thus the familial patterns do suggest a genetic influence, but the nature of that influence is not yet clear.

Although synaesthesia is described as an atypical neurological condition, those who experience synaesthesia do not regard it as a perceptual or cognitive deficit. On the contrary, many individuals with synaesthesia consider the condition to be a gift, and cannot imagine a life lacking in their atypical

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perceptual experiences. In fact, synaesthetes outperform controls on some perceptual tasks related to the sensory modality in which they experience synaesthesia. For example, those with colour-grampheme synaesthesia have better colour vision, colour memory, and word memory than controls (Banissy *et al.* 2009; Yaro and Ward 2007), and those with sequence-form synaesthesia have better memory for the timing of world events and are better on tasks requiring the manipulation of units of time or space (Mann *et al.* 2009; Simner *et al.* 2009b; but see Ward *et al.* 2009, for slower mathematical operations in this form of synaesthesia). In addition, synaesthesia may facilitate certain types of creativity and artistic pursuit (Rich *et al.* 2005; Ward *et al.* 2008).

10.3 Perceptual reality

For non-synaesthetes, the idea of a synaesthetic experience is difficult to conceive. As such, the condition has long been viewed as a curiosity that might arise from overly active imagination (Hubbard and Ramachandran 2005), and the last century has seen intense debate concerning the perceptual reality of synaesthesia. Recently, a variety of behavioural and neuroimaging methods have verified the validity of the synaesthetic experience.

10.3.1 Behavioural evidence

One type of behavioural evidence establishing the perceptual reality of synaesthesia is the consistency of reported percepts over time. For example, in one study 26 adults with coloured-hearing synaesthesia and 23 controls matched specific sounds to their choice of 238 calibrated colour swatches. When retested at least one month later, the synaesthetes' consistency was more than twice as high as that of the controls, who had been instructed to remember their choices until their retest one week later (Asher *et al.* 2005). Such high consistency has been found in other studies of coloured-hearing synaesthesia, as well as in studies of sequence-form synaesthesia, word-taste synaesthesia, and coloured-grapheme synaesthesia (e.g. Baron-Cohen *et al.* 1993: Dixon *et al.* 2000; Eagleman *et al.* 2007; Edquist *et al.* 2006; Smilek *et al.* 2007b; Ward *et al.* 2006; Ward and Simner 2003). Typically, even the most consistent control subject does not approach the range of consistency shown by the synaesthetic group. In fact, the consistency of reported synaesthetic experiences over time has come to be known as the behavioural gold standard for assessing the reality of the condition (Cytowic 1989).

Stroop-like interference paradigms have demonstrated the automatic and obligatory nature of synaesthetic percepts. In a traditional Stroop task, participants are asked to name the ink colour of colour words printed in a consistent (red printed with red ink) or inconsistent (red printed in green ink) colour (Stroop 1935). Participants' longer response times and more frequent errors on inconsistent trials indicate that the automatic decoding of word meaning interferes with naming the colour of the ink. Similar interference occurs when synaesthetes with coloured hearing are asked to name the colour of a visual patch while ignoring irrelevant tones that induce consistent ↳ colours (a green-inducing tone at the same time as a green visual patch) or inconsistent colours (a red-inducing tone with the green patch). Individuals with coloured hearing are significantly slower on inconsistent trials than on consistent trials, a pattern suggesting that the synaesthetic colour elicited by the tone occurs automatically and interferes with, or slows down, the perception and naming of the actual ink colour (Ward *et al.* 2006). Similar Stroop-like interference occurs in synaesthetes with coloured graphemes when they are shown letters or digits printed in colours consistent or inconsistent with their synaesthesia and are then asked to name the colour of ink while ignoring the letter (Dixon et al. 2000; Mills *et al.* 1999; Mattingley *et al.* 2001; Mattingley *et al.* 2006; Nikolic´ *et al.* 2007; Rich and Mattingley 2003; Ward *et al.* 2006).

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Synaesthetic crossmodal percepts also cue visual attention in a manner that suggests that they are perceptually valid. For example, when synaesthetes with coloured hearing are exposed to a tone while observing an array of colour patches, their attention is cued toward the visual patch matching the colour induced by the sound, as evidenced by their faster detection of targets in that location (Ward *et al.* 2006). Similarly, when individuals with sequence-form synaesthesia are asked to detect targets appearing in various locations in visual space, each preceded by an irrelevant digit, they are faster if the digit is one that is perceived synaesthetically in the same location as the target than if it is perceived as located elsewhere (Jarick *et al.* 2009). Akin to data on consistency over time, the behavioural findings on Stroop interference and attentional cueing suggest that synaesthetic percepts behave like typical, non-synaesthetic percepts, further establishing the perceptual reality of the phenomenon.

10.3.2 Neuroimaging evidence

Neuroimaging evidence has also played a role in establishing synaesthesia as a genuine perceptual phenomenon. Studies using functional magnetic resonance imaging (fMRI) have demonstrated that stimuli reported to induce specific synaesthetic percepts elicit brain activity in regions known to be involved in the processing of those perceptual characteristics. For example, an fMRI study with coloured-hearing synaesthetes and non-synaesthetic controls showed that spoken words elicited activations in areas V4 and V8 of the visual cortex (human colour area) in synaesthetes, but not controls (Nunn *et al.* 2002; see also Paulesu *et al.* 1995, for similar results from positron emission topography). Subsequent fMRI studies have replicated this V4/V8 activation in response to words, as well as, in some studies, other parts of the visual pathway and areas of the parietal cortex known to be involved in the binding of colour to shape in typical perception (Gray *et al.* 2006; Hubbard *et al.* 2005; Stevens *et al.* 2006; Witthoft and Winawer 2006). In other words, for synaesthetes with coloured hearing, hearing words activates not only the auditory and lexical pathways, but also pathways normally involved in the processing of colour and its linking to shape. In a similar study of a synaesthete who tastes words ('Philip' evokes the taste of 'oranges not quite ripe'), listening to words caused the typical activation in lexical decoding areas, but, crucially, also caused activation in the primary gustatory cortex that is active during the experience of taste in the typical brain (Ward and Simner 2003). Similar conclusions come from fMRI studies of coloured-grapheme synaesthetes and non-synaesthetic controls who have been presented with arrays of achromatic digits. All participants show activation in the grapheme area of the cortex, however synaesthetes also show activity in visual colour area V4, with some reports of activity in lower visual areas and in a number of higher cortical areas, including the intraparietal sulcus (Hubbard *et al.* 2005; Rouw and Scholte 2007, 2010; Sperling *et al.* 2006; but see Rich *et al.* 2006). A role for the parietal cortex in the induction of this form of synaesthesia was confirmed in two studies using transcranial magnetic stimulation (TMS): Temporarily interrupting parietal cortex activity reduced the Stroop-like interference between real-world and synaesthetic colour (Esterman *et al.* 2006; Muggleton *et al.* 2007). Combined, the fMRI and TMS results provide ↳ strong evidence that the reported synaesthetic percepts are mediated by neural pathways active during real-world perception of the same stimuli.

10.4 Hypothesized developmental origins

There are two main hypotheses about the developmental origins of synaesthesia: cross-activation of cortical areas because of:

- less-than-normal pruning of the exuberant connections that are prevalent during early development
- less-than-normal development of inhibition of such connections.

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There is evidence to support each hypothesis, and they may well both contribute to the manifestation of synaesthesia. What is important for this chapter is that both hypotheses represent an atypical playing out of a normal developmental process. Hence, both hypotheses imply that the neural substrate for unusual connections among dimensions and modalities exists in the typically developing child and may persist in muted form in typical, non-synaesthetic adults. In this section, we review the evidence for each hypothesis and its relationship to the normal developmental process.

10.4.1 Pruning

In typical adults, each sensory cortical area is specialized for the processing of information from one sensory system. However, that is the end point of a developmental process that begins with an exuberant production of synapses, including ones between sensory cortical areas. During development, these exuberant synapses undergo experience-dependent pruning, such that stimulated synapses are strengthened and refined, while inactive synapses are pruned. As a result of this process, each sensory cortex becomes tuned to a single modality because it receives the strongest and most coherent input from that sense. The temporary connections are most likely to form between contiguous cortical areas. Whilst exuberance and pruning appear to be ubiquitous processes, their timetables differ across species and sensory modalities (e.g. Bourgeois and Rakic 1993; Dehay *et al.* 1984; Huttenlocher 1984). In the cat, such exuberant connections form during infancy among primary visual, auditory, and somatosensory cortices, but during development these synapses are pruned so that these areas become unisensory areas (Dehay *et al.* 1988). In the monkey, such ubiquitous exuberance has not been observed, but there is evidence of the formation of connections during infancy from primary auditory cortex to visual area V4, the area active during coloured hearing and coloured grampheme synaesthesia (see Section 10.3.2), connections that are no longer observed in the brain of the adult monkey (Kennedy *et al.* 1997).

In humans, there is indirect evidence for a similar developmental process of over-production of synapses and experience-dependent pruning. Anatomical tracing has revealed a process of over-expression of dendritic spines early in life followed by a reduction to adult levels in every cortical area, although the timing of the peak over-production and subsequent pruning varies across cortical areas, and even between layers within each area (e.g. Huttenlocher 1984). A similar pattern emerges in measurements of the levels of glucose utilization, which reflect the metabolic demands of neural activity; for example, there is an increase in glucose utilization in sensory cortical areas over the first 3–4 years of life, which is followed by a plateau and a subsequent decrease beginning at about age 9 (Chugani 1994; Chugani and Phelps 1986; Chugani *et al.* 1987).

Comparisons of cortical specialization in normal, blind, and deaf adults indicate that this pruning is experience-dependent. When normal input is missing, for example because of congenital blindness or deafness, the normal development of unimodal specialization of the visual and auditory cortices fails to occur. In the congenitally blind, the adult visual cortex ↳ responds to auditory, tactile, and language input, and interference by TMS degrades performance (reviewed in Spector and Maurer 2009b). Studies of adult cats that were blinded at birth (by removing the eyes) indicate that the visual cortex failed to develop its normal specialization; instead, the visual cortex contains neurons that give well-tuned responses to auditory stimuli (inputs from other modalities have not been tested) (Yaka *et al.* 1999). Similarly, in humans with congenital deafness, the adult auditory cortex responds to both visual and tactile stimulation (reviewed in Spector and Maurer 2009b).

Together, these studies suggest that unisensory cortical areas become specialized as a result of dominant input from a single sense, leading to strengthening and refinement of direct sensory connections and the pruning away of the initially prevalent connections from other senses. When the dominant input is missing

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because of deprived input, such as deafness or blindness, no such specialization occurs, and the area remains multisensory in adulthood.

There is indirect evidence that yet-to-be-pruned crossmodal connections are functional in early childhood. For example, in young infants, human speech elicits event-related potentials over the auditory cortex, as it does in adults. However, unlike in adults, speech also elicits strong responses over the visual cortex, which gradually diminish over the first three years of life (Neville 1995). In newborns, tactile stimulation of the wrist elicits an evoked response over the somatosensory cortex, as it does in adults. However, unlike in adults, the response is larger when white auditory noise accompanies the tactile stimulation (Wolff *et al.* 1974). Similarly, PET (positron emission tomography) data reveal that even the response to human faces is not as localized early in life as it is in adults. For example, similar to adults, 2-month-olds who looked at faces and a control visual stimulus of Christmas tree lights exhibited more activity in response to faces in the right inferior gyrus, close to the classic fusiform face area of adults. Unlike adults, however, there was also more activity in the left auditory cortex and left Broca's area, areas that later become specialized for hearing and language (Tzourio-Mazoyer *et al.* 2002). Together with the evidence for congenital blindness and deafness, these findings suggest that the human cortex is not initially subdivided into specialized unisensory areas, but instead that unisensory cortical areas develop postnatally in response to the patterns of environmental input received.

There is also indirect evidence for early functional interconnection among visual pathways that will later become segregated and specialized. For example, in adults, the initial processing of motion and colour occur via distinct, parallel pathways, such that the motion system appears to be largely 'colour-blind'. One demonstration of this is that adults can readily report the direction of moving stripes if they are formed by contrasting luminance (e.g. light and dark stripes), but not if the stripes are formed by equiluminant contrasting colours (e.g. red and green stripes). Young infants 2–4 months old, however, are equally proficient at seeing moving stripes that are defined by luminance or by colour, suggesting that colour pathways initially have connections to the motion pathway that are later retracted (Dobkins and Anderson 2002). Thus, in the infant brain, colour processing appears not yet to be confined to specialized networks.

Combined, these studies suggest that initially there are connections among and within sensory cortical areas that are pruned during development in an experience-dependent manner. These extra connections are most prevalent during early childhood, and exactly when they diminish to adult levels likely varies with respect to the cortical areas they connect. The initial exuberant connections are likely to be fairly local, such as those connecting contiguous brain areas. Indirect evidence on timing comes from studies of glucose metabolism and fibre tracking. The increased levels of local connectivity, revealed by glucose metabolism to be present in early childhood, do not begin to decline toward adult levels until around age 9 years (Chugani *et al.* 1987). A similar conclusion comes from recent studies tracing interconnected areas based on similar fluctuations in resting state metabolism, confirmed by fibre tracking with DTI (diffusion tensor imaging); both methods indicated that as late as age 7–9 years, local connectivity is stronger in children than in adults (Fair *et al.* 2009; Supekar *et al.* 2009).

The 'pruning' hypothesis of synaesthesia explains the phenomenon as the result of less-than-normal pruning of the exuberant connections seen in early development; some of the connections are posited to remain functional and influence conscious perception (e.g. Maurer and Maurer 1988; Ramachandran and Hubbard 2001). As would be expected from the normal developmental process, manifestations of synaesthesia often involve inductions between contiguous brain areas; colour may often be induced because areas V4 and V8 that are involved in its mediation lie amidst many other brain areas. Also, as atypical synaptic pruning would likely not be restricted to one cortical area, many synaesthetes have more than one form of synaesthesia. However, there is no explanation of what might cause less-than-normal pruning to occur or, further, why it affects some connections between contiguous areas and not others.

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The pruning hypothesis predicts that synaesthetes will exhibit more-than-normal neural connections between cortical regions involved in their atypical perceptions. There is evidence from MRI (magnetic resonance imaging) and DTI indicating increased grey and white matter, respectively, in the expected areas. For example, a study of synaesthetes with coloured hearing observed increased cortical thickness, surface area, and volume throughout the ventral visual pathway where colour is processed, as would be expected if there were increased connectivity because of reduced pruning (Jäncke *et al.* 2009). Importantly, this experiment also uncovered a possible difference between associator and projector synaesthetes, in that both groups had increased grey matter volume in the left parietal cortex, which is implicated in the binding of colour to shape, but only projectors showed the increases in the visual cortex, along with increases in auditory, motor, and superior frontal areas (Rouw and Scholte 2010). Associators, on the other hand, showed increased grey matter volume in the hippocampus. An MRI study of 18 individuals with coloured-grapheme synaesthesia and 18 matched controls also found evidence consistent with increased volume from decreased pruning (Weiss and Fink 2009). The synaesthetes had increased density of grey matter in the right fusiform gyrus, near the V4 colour area and visual word form area, and correlated increases in the left intraparietal sulcus, near hIP3, an area known to be involved in the multisensory processing that links colour and form. A DTI study of individuals with coloured-grapheme synaesthesia revealed evidence of increased volume of white matter fibre tracts, compared to matched controls, in three areas:

- in a visual word form area in the right inferior temporal cortex next to an area in the fusiform gyrus implicated in colour processing
- in areas in the left parietal cortex implicated in the binding of colour to form
- in the superior frontal cortex (Rouw and Scholte 2007).

Interestingly, the volume differences in the visual word form area were greater for projector than associator synaesthetes. Similar patterns (increased fibre tracts and grey and white matter volume) were found in auditory, gustatory, and visual areas in a synaesthete with both coloured hearing and an usual form of synaesthesia in which specific tone intervals induce specific tastes (e.g. a minor second tastes sour; Hänggi *et al.* 2008).

The DTI and MRI findings converge nicely with fMRI evidence of activity in area V4 and in the fusiform gyrus in individuals with coloured hearing and coloured-grapheme synaesthesia (e.g. Hubbard *et al.* 2005; Rouw and Scholte 2010; Stevens *et al.* 2006) and its suppression when TMS is applied to the parietal cortex, at least on the right (Esterman *et al.* 2006; Muggleton *et al.* 2007; see Section 10.3.2). It is in those areas that there is consistent evidence across studies of increased cortical thickness and white matter tracts. The DTI and MRI evidence for increased fibres/thickness in the superior frontal cortex was unexpected, and might reflect the effort needed to ↳ constantly distinguish between synaesthetic and veridical perceptions. Also unexpected was the evidence for changes in hippocampal memory networks in associators.

10.4.2 Inhibition

The second hypothesis about the origins of synaesthesia proposes that the condition arises from altered feedback from higher cortical areas onto lower sensory cortical areas (Grossenbacher and Lovelace 2001). In the typical adult, this feedback strengthens the firing of neurons responding coherently to the perceptual properties of a stimulus and inhibits the firing of more isolated neurons. For example, this process will facilitate the continued firing of neurons in the primary visual cortex tuned to diagonal orientations when viewing the letter X, while simultaneously inhibiting the firing of neurons tuned to horizontal and vertical orientations. In synaesthesia, according to this account, some of this inhibition is disinhibited, resulting in extra firing, including that elicited by any remnants of the exuberant connections of early childhood among dimensions (e.g. colour and motion) or modalities (e.g. vision and hearing).

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Note that this account assumes that not all of the exuberant connections are eliminated by pruning, but rather that some connections remain that are normally inhibited. Indeed, in adult monkeys, neurons in the primary visual cortex with receptive fields in the visual periphery receive direct input from the primary auditory cortex (Falchier *et al.* 2002), and responses of neurons in monkey auditory cortex are modulated by simultaneous visual input (Bulkin and Groh 2006). Indirect evidence for such connections in the typical human adult comes from studies of blindfolded adults. For example, after 5 days of blindfolding to remove the normal, dominant visual input, the visual cortex became active during tactile and auditory discriminations, and interference with visual cortex activity by TMS (transcranial magnetic stimulation) disrupted tactile discrimination (auditory discrimination was not tested; Pascual-Leone and Hamilton 2001). These findings suggest that some direct crossmodal connections between sensory cortical areas remain in the typical adult brain, but that these connections are normally sufficiently inhibited to have no effect on conscious perception. They nevertheless can have indirect effects on adults' perception (see Section 10.5). Note that during normal development, such crossmodal connections will be more prevalent and are less likely to be inhibited (e.g. Burkhalter 1993).

By this account, synaesthesia arises not from a lack of pruning, but from a failure to inhibit remaining crossmodal and cross-dimensional connections. As with pruning, there is no explanation of what causes synaesthetes to develop less-than-normal inhibition. The 'inhibition' explanation of synaesthesia predicts that it should be possible to induce synaesthesia in non-synaesthetes by reducing inhibitory feedback. Indeed, it is possible to elicit reports of synaesthesia in typical, non-synaesthetic adults through hypnosis (Cohen Kadosh *et al.* 2009) and ingestion of LSD (Aghajanian and Marek 1999), although the mechanism has not been established, nor whether what is induced has all the hallmarks of synaesthesia, including consistency, automaticity, and modulation by TMS.

10.4.3 Role of experience

Synaesthetes report that they have had extra synaesthetic percepts 'all their lives'. Nevertheless, many forms of synaesthesia must have emerged postnatally, as they are elicited by culturally learned stimuli such as the letters of the alphabet, days of the week, or specific words. One possibility is that before learning such stimuli, synaesthesia was manifested in a different, but related, form—as a connection, for example, between basic shapes and colour (a prelude to coloured graphemes), between sequences of daily events and spatial locations (a prelude to sequence-form ↳ synaesthesia), or between specific combinations of sounds and taste (a prelude to lexical-gustatory synaesthesia). This possibility is supported by the early drawings of words made by one coloured-grapheme synaesthete before she learned to read (Duffy 2001): She drew coloured patches resembling a primitive Mondrian. Because of reduced pruning and/or inhibition, individuals predisposed to synaesthesia may experience extra percepts automatically as they learn the alphabet, learn to read, taste new foods, hear new musical notes, etc. From the synaesthete's perspective, the additional percepts have been there 'always'; that is, always when the individual was exposed to the inducing stimulus. The specific synaesthetic perceptions may be influenced by couplings encountered in the child's environment, such as the colour of shapes (e.g. letters on refrigerator magnets). Because the child has less than typical pruning or inhibition, those couplings may be retained and become perceptual in nature, unlike the fleeting effect they have on typical children (Witthoft and Winawer 2006). However, for most synaesthetes with coloured graphemes, no environmental source for the specific idiosyncratic mappings can be found, despite perusal of children's books and the child's toy box in search of coloured letters or digits to which they were or might have been exposed (Rich *et al.* 2005). Indeed, in an ongoing study of three preschool children with colour-grampheme synaesthesia, we have found no correspondence between the colours they report perceiving for each letter of the alphabet and anything in their home environment (Spector and Maurer unpublished data).

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When a stimulus induces a synaesthetic experience early in development during the period of experience-dependent pruning, rather than being encountered for the first time later in development, the underlying neural connections should be strengthened by their co-activation and lead to the establishment of a stronger synaesthetic percept. For the same reason, inducers encountered frequently during development should lead to stronger percepts than those encountered infrequently. With the reinforcement of these neural connections by their co-activation, one would expect the elicited synaesthetic percepts to become stronger, more consistent, and more easily transferred to similar forms or sounds or associated stimuli (Mroczko *et al.* 2009). Indeed, in young children showing signs of colour-grampheme synaesthesia, the consistency of the reported associations increases between age 3.5 and 5.5 years (Spector and Maurer 2009a) and after 1 year of school (Simner *et al.* 2009a). Data from adults with coloured-grapheme synaesthesia are also consistent with these predictions: low numbers (1, 2, 3—the numbers that children learn first) and high-frequency letters elicit brighter synaesthetic percepts (Beeli *et al.* 2007; Cohen Kadosh *et al.* 2009; Simner 2007; Smilek *et al.* 2007a; Smith and Sera 1992). In contrast, when a new category of inducer is encountered in adulthood (e.g. a new alphabet), new synaesthetic percepts may arise, but they are usually less strong than existing ones (Mills *et al.* 2002; Ward and Simner 2003).

Efforts to induce synaesthesia by training in typical adults have proven unsuccessful. Non-synaesthetic adults have learned to associate letters or digits with specific arbitrary colours after many hours of training in the laboratory and after studying consistent patterns linking numbers to colours in cross-stitch needlepoint (Elias *et al.* 2003; Meier and Rothen 2009). After training, these associations cause a congruency effect on Stroop tasks, much like genuine synaesthetes; but, unlike synaesthetes, trained non-synaesthetes do not report experiencing synaesthetic percepts, the letters do not evoke responses conditioned to the colours, and extra-striate visual areas are not activated when doing mental manipulations with the inducers (e.g. mental arithmetic with trained digits; Elias *et al.* 2003; Meier and Rothen 2009). Thus, synaesthesia cannot be induced by training in typical, non-synaesthetic adults. Nevertheless, in those with synaesthesia, the individual's developmental history of encountering inducers and specific associations can affect the specificity and strength of their synaesthetic percepts.

10.4.4 Which correspondences?

It is not clear why each individual synaesthete develops an idiosyncratic set of specific correspondences, either a specific form of synaesthesia (e.g. coloured letters or coloured tones) or the specific set of correspondences within that form (e.g. middle C as red or pink). However, common patterns across synaesthetic perceptions in adults with synaesthesia and the crossmodal associations of adults without synaesthesia indicate that some specific correspondences are more likely than others. These similarities may be related to the systematic organization within each sensory cortical area, such that neurons with similar tuning preferences lie closest to each other and farthest from neurons with the orthogonal tuning. Hence any mapping between contiguous cortical areas is likely to link neurons with one set of preferences in one domain (e.g. high auditory frequency) to neurons with a particular set of preferences in another domain (e.g. jagged shape). As discussed in Section 10.4.3, idiosyncratic exposure to crossmodal or cross-dimensional associations in the environment (e.g. coloured letters on fridge magnets) may also influence the specific mappings acquired.

10.5 Implications for development

The hypothesis that incomplete pruning and/or inhibition lead to synaesthesia has three implications for the development of the typical non-synaesthetic child.

1. Before the completion of experience-dependent pruning within and between sensory cortical areas, the

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child should show synaesthetic-like crossmodal and cross-dimension associations.

2. Even in adulthood, there may be remnants of these earlier associations because the pruning and/or inhibition are not complete.

3. There will be similarities in the cross-dimensional and crossmodal percepts of synaesthetic adults and the associations of typically developing children and non-synaesthetic adults.

Recent studies have documented many instances supporting the third prediction by showing similarities between synaesthetic and non-synaesthetic adults (for a review see Spector and Maurer 2009b). In this section, we concentrate on the associations that have also been shown in young children. Some of these associations may be based on early learning because they match environmental statistics (high pitch = small size; e.g. mice squeak and lions roar; children have higher pitched voices than adults) or appear only later, after the child has had many years to learn crossmodal and cross-dimensional correspondences in the environment and begun to acquire culturally-specific knowledge, like the spelling of words (e.g. the letter 'b' goes with blue). Other correspondences, however, have no ready learning explanation and are already present in infancy or toddlerhood (e.g. high pitch = sharp and bright). Rather than learning, these associations appear to reflect natural associations favoured by the intrinsic wiring of the nervous system.

10.5.1 Magnitude mapping: loudness—lightness

Newborn infants appear to match louder sounds to brighter lights and softer sounds to darker lights. Thus, after habituation to a bright patch of light, newborns show less heart rate response to an intense sound; after habituation to a dark patch, they respond less to a soft sound—as if they translated the magnitude of the light stimulation into auditory magnitude and generalized habituation across domains (Lewkowicz and Turkewitz 1980). Such magnitude mapping is common in adults, in whom it is manifest in situations as diverse as judging the duration of notes (longer if accompanied by a larger gesture), the loudness of white noise (louder if accompanied by light), ↳ the sweetness of sugar water (sweeter if redder), or the intensity of odour solutions (more intense if coloured, even if the colour is wrong, e.g. green strawberry) (Johnson and Clydesdale 1982; Odgaard *et al.* 2004; Schutz and Lipscomb 2007; Stein *et al.* 1996; Zellner and Kautz 1990; reviewed in Spector and Maurer 2009b). Although the common code for magnitude may be learned (e.g. larger objects do tend to make louder sounds), the evidence for magnitude matching at birth suggests it may instead, or in addition, be based on a natural bias in the associations between sensory modalities that is independent of environmental learning. By natural bias, we mean that the association may develop from general developmental processes rather than the learning of statistical regularities in associations present in the environment.

10.5.2 Visual associations to pitch

Pitch is an interesting dimension for the investigation of these questions because it is metathetic: unlike brightness and loudness, it has no obvious end that is of greater magnitude—adults do not agree on whether treble tones are more or less than bass tones; indeed, our labelling of treble tones as higher pitch is an arbitrary convention of our language. There are a number of common association to pitch:

A) *Sharpness.* Adults with coloured hearing report that lower pitches evoke rounder visual images and higher pitches evoke more pointed images (Marks 1974), an association that affects the associations of non-synaesthetic adults as well. For example, non-synaesthetic adults pick a tone of a lower pitch as the most suitable match for a rounder shape (O'Boyle and Tarte 1980), and they are faster and more accurate to report that a visual form is round rather than pointed if it is accompanied by an irrelevant tone of lower rather than higher pitch (Marks 1987). In fact, when asked to judge whether a shape or sound was

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presented first, the accuracy of non-synaesthetic adults decreases when a higher pitched sound occurs just before an angular, rather than rounded shape, as if the congruent mapping fuses the sound and shape together so that the participant can no longer judge accurately which one came first (Parise and Spence 2009). The same association has been demonstrated in infants just 3–4 months old. Infants looked longer at a visual display when a shape morphing from an amoeboid to a pointed version was accompanied by a whistle sound increasing in pitch than at a display with the reverse mapping (Walker *et al.* 2010). These babies had 3–4 months of postnatal experience during which they would have been exposed to many auditory-visual combinations, some spurious coincidences (e.g. mother enters room as telephone rings) and some representing environmental correspondences (e.g. mother's moving lips and mother's voice). Nevertheless, there is no obvious environmental link between rounder objects and lower pitches or pointed objects and higher pitches (e.g. faces, one of the stimuli infants encounter most often, are round and come with voices covering a large range of pitches). Thus, it seems likely that the correspondence between pitch and sharpness is a natural bias arising from intrinsic connections between visual and auditory brain areas.

B) *Height.* Adults also associate lower pitches with lower positions in space and higher pitches with higher positions in space: they judge a lower pitched sound to be coming from a lower position in space (Roffler and Butler 1968) and make judgements about both location and pitch faster if the other dimension is congruent (Melara and O'Brien 1987). Infants 3–4 months of age appear to make the same association: they look longer at a visual display when an orange ball moves up the screen as the pitch of the accompanying whistle tone increases than at the visual display with the reverse mapping (Walker *et al.* 2010). These associations are not likely to have been learned from the infants' environment over the first 3–4 months. For example, babies do not yet know that we refer to treble tones as higher pitched and that ↳ taller people (e.g. Dad) have voices with lower pitch than shorter people (e.g. mother, older sister), which is just the opposite mapping. Instead, the results suggest that there are natural associations between pitch and visual characteristics that arise from the intrinsic wiring of the nervous system.

C) *Lightness.* Synaesthetic adults experience brighter percepts in response to sounds of higher pitch (e.g. a higher-pitched C elicits a brighter red than the duller red evoked by a lower-pitched C) (Marks 1974; Ward *et al.* 2006). Likewise, non-synaesthetic adults match tones of higher pitch to lighter colours and judge both pitch and lightness more accurately if a distracter on the other dimension is congruent (e.g. darker light with lower pitched distracting noise) (Marks 1974). Toddlers (2.5–3 years of age) demonstrate the same pitch–lightness correspondence as adults. This was shown in a study in which toddlers observed two simultaneously bouncing balls, one light and one dark, accompanied by a lower-pitched or higher-pitched sound. When asked which ball was making the noise, toddlers consistently matched the lower-pitched sound to the darker ball and the higher-pitched sound to the lighter ball (Mondloch and Maurer 2004). This correspondence between pitch and lightness is unlikely to arise from experience with the association in the environment, as lighter objects do not consistently make higher pitched sounds in the world (e.g. a brown mouse squeaks at the same pitch as a white mouse). Thus, pitch and lightness seem to connect crossmodally in a way that could be naturally-biased by cortical connectivity among neighbouring sensory cortical areas.

D) *Size.* Toddlers connect higher pitch to smaller visual stimuli (Mondloch and Maurer 2004), just like the perceptual matches of non-synaesthetic adults and the induced percepts of adults with synaesthesia (Marks 1974). This correspondence also influences adults' judgments of the temporal order and spatial contiguity of a sound and visual stimulus: when a higher-pitched sound occurs on the same trial as a smaller visual stimulus, adults are more likely to misjudge which one came first and which one is displaced to the right, as if the correspondence melded the pitch and shape together (Parise and Spence 2009). This could be an additional example of a natural bias, or it might arise from experience, as larger organisms tend to make lower pitched sounds (e.g. mice squeak and lions roar and children have higher

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pitched voices than adults). Alternatively, it could result from a dynamic interplay of natural biases and learning. For example, there may be an initial natural bias to associate high pitch with lightness and smallness, which would help the developing child to understand the statistics of the environment. Learning these statistics would reinforce the strength of this association as the child gains experience in a world where smaller organisms tend to make higher pitched sounds. Indeed, studies of older children indicate gradually increasing understanding of this correspondence throughout middle childhood (Marks *et al.* 1987).

In sum, young children associate higher and lower pitch to polar opposites along the visual dimensions of sharpness, height in field, surface lightness, and size. We hypothesize that the matching for sharpness, height in field, and surface lightness represent examples of crossmodal mappings that cannot readily be explained by learning because the correspondence is not prevalent in the environment. The matching for size might be acquired early from the observation of statistical regularities in the environment or it, too, might start out as a natural bias that can be modified by learning.

10.5.3 Colour—letters

Coloured graphemes is one of the most common forms of synaesthesia (see Section 10.1). If young children have more synaesthetic-like perception before experience-dependent pruning ↳ and the development of inhibitory feedback, then it might be possible to observe perceptual manifestations of synaesthesia early in development. Dobkins (2011) tested this hypothesis by investigating whether young infants behave as if circular and diamond shapes have distinct colours. To do so, she showed infants a field of circles (or diamonds) on a background, half of which was red and half of which was green. She reasoned that for any given baby, these two shapes might induce different colours, so that circles would be easier to see against one colour of background and diamonds against the other. Indeed, she found non-random choices across trials consistent with synaesthetic perception at 2 months of age for red/green and at a slightly older age for yellow/blue, as would be expected given that it is known that the yellow/blue channels develop more slowly than the red/green channels. These results provide the first direct evidence that stimuli that act as inducers for adult synaesthetes may not only elicit crossmodal associations of the same type in infants, but actually elicit synaesthetic percepts that are superimposed on the world.

Some of these early colour-shape associations appear to persist in typical adults as well as in adults with synaesthesia. While each individual colour-grampheme synaesthete has a unique coloured alphabet, there are some letters of the alphabet that tend to be associated to the same colours at above chance levels across synaesthetes (e.g. ~40% of synaesthetes report that A is red; Day 2004; Rich *et al.* 2005; Simner *et al.* 2005). Likewise, non-synaesthetic adults do not typically associate letters to colours, but when asked to do so, they tend to agree on the colour of some letters of the alphabet, in large part the same ones for which synaesthetes with coloured graphemes show consistency (Rich *et al.* 2005; Simner *et al.* 2005). Some of these consistent letter–colour associations appear to be based upon literacy. For example, English-speaking participants commonly associate G to green. However, some of the consistent letter–colour associations cannot be readily explained by literacy. For example, at levels far exceeding chance, both synaesthetic and non-synaesthetic English-speaking adults associate X and Z with black; O and I with white, and C with yellow (Barnett *et al.* 2008; Day 2004; Rich *et al.* 2005; Simner *et al.* 2005).

Despite the early colour–shape connections observed in infants, one might expect differences in colour–shape connections between infants, children, and adults for whom those shapes have become letters of the alphabet they use in reading. Consistent with this prediction, adults and children 7 to 9 years of age who have begun to read, but not toddlers, consistently associate letters to colours when there is an apparent literacy basis for their mapped colours in adults (A/red and G/green, B/blue and Y/yellow; Spector and Maurer 2008, 2011). However, in some cases where the adult associations do not have a ready literacy

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explanation, toddlers made the same colour–shape associations as are common in synaesthetic percepts and typical adult crossmodal associations: they expected X and Z to be hidden in a black box and I and O to be hidden in a white box. Further, the consistent matching for I, Z, X and O was based upon the shape and not the sound of the letter, and appeared to be related to the angularity of the shape: toddlers searched for jagged shapes in the black box and rounded shapes in the white box. In addition to the associations of smooth shapes to white and jagged shapes to black, toddlers, like synaesthetic and non-synaesthetic adults (Day 2004; Rich *et al.* 2005; Simner *et al.* 2005), associated C with yellow (Spector and Maurer 2011). As suggested earlier, these early associations may result from naturally biased associations between shape and colour that reflect intrinsic cortical connectivity among neighbouring sensory cortical areas. These connections seem to persevere into adulthood, as shown by the persistence into adulthood of the associations not readily explained by literacy (O and I/white; X and Z/black; C/yellow) (Day 2004; Maurer and Spector 2011; Rich *et al.* 2005; Simner *et al.* 2005) and their commonness in the actual synaesthetic percepts of adults with coloured grapheme synaesthesia (Day 2004; Rich *et al.* 2005; Simner *et al.* 2005). Furthermore, while sensory cortical organization may initially bind colour to shape, the development of literacy can induce ↳ additional associations, as shown by the emergence around age 7 in English-speaking children of the association of A to red, B to blue, Y to yellow, and G to green, perhaps as a result of differential recruitment of higher order networks as letters take on meaning (Spector and Maurer 2011).

10.5.4 Sound—shape (sound symbolism)

Our final example examines whether intrinsic crossmodal associations may influence the development not only of perception but of language as well. It originated from evidence that typical adults have biases to associate specific sounds to specific shapes (Ramachandran and Hubbard 2001; Kohler 1929; Lindauer 1990; Marks 1996). For example, when asked to match the nonsense words ‘takete’ and ‘maluma’ to rounded and jagged shapes, most people answer that the jagged shape is ‘takete’ and the rounded shape is ‘maluma’ (Kohler 1929; Lindauer 1990). This effect has been replicated with modified shapes and words (e.g. kiki and bouba) in experimental studies with English-speaking adults and with 8–14-year-old children who spoke Swahili and the Bantu dialect of Kitongwe, but not English (Davis 1961; Holland and Westheimer 1964; Ramachandran and Hubbard 2001). Researchers speculate that these phenomena arise from connections among contiguous cortical areas mediating decoding of the visual percept of the nonsense shape (round or angular), the appearance of the speaker’s lips (open and round or wide and narrow), and the feeling of saying the same words oneself (e.g. Sapir 1929; Ramachandran and Hubbard 2001). They argue that these connections lead to natural mappings between sound and shape that sometimes result in synaesthesia but which are present in some form in everyone. These naturally-biased associations may also influence the language development of an individual child by contributing to the ease with which the child learns semantic mappings. The relationship between the natural mappings and the semantics of the language will be one of mutual influence: as the child acquires the vocabulary of the language some of the natural correspondences between shape and sound will be reinforced and others will be altered because they are not common in the child’s language (see Nuckolls 1999; Smith and Sera 1992). The natural mappings may also have influenced the evolution of languages, and may explain why adults are able to guess the meanings of foreign words from remotely related languages at rates exceeding chance (Berlin 1994), with even higher accuracy if the words match in meaning (Nygaard *et al.* 2009) or are chosen based on sound symbolism (Imai *et al.* 2008).

The maluma/takete mapping has usually been attributed to the contrast between rounded and unrounded vowels. A vowel is considered rounded or non-rounded based upon the shape of the mouth and the lips when pronouncing it. For example, for the phoneme [o], as in ‘code’, the mouth is wide open and the lips are rounded and slightly protruded, whereas for the phoneme [i], as in the word ‘feet’, the mouth is partly closed and the corners of the lips are drawn back (Dale 1976). In two recent studies, we assessed whether

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language-learning toddlers associate nonsense words with rounded vowels to unfamiliar rounded shapes and nonsense words with non-rounded vowels to unfamiliar angular shapes. This was tested using a game in which English-speaking toddlers were presented with four pairs of nonsense words, in which one word contained rounded vowels and the other word contained non-rounded vowels. Children were asked to choose which of two unfamiliar shapes (one round and one angular) corresponded to one of the words in each pair. The contrasting shapes were ones known to be optimal for selectively stimulating neurons in cortical area V4, the area active during forms of synaesthesia that involve sound (see Section 10.3.2). As predicted, toddlers, like the non-synaesthetic control adults, associated the nonsense words that contained non-rounded vowels (e.g. tee-tay; tuh-kee-tee, gee gee, dee-dee) to the jagged shapes and the nonsense words with rounded vowels (e.g. go-gaa, maa-boo-maa, go-go, do-do) to the rounded shapes (Maurer *et al.* 2006; Spector and ↳ Maurer, in preparation). In toddlers, there was no influence of contrasting stop versus approximate consonant sounds (e.g. bibi versus yiyi) on matching to jagged versus rounded shapes (Spector and Maurer, in preparation). The unifying influence might well be pitch: pitch tends to be higher when pronouncing non-rounded vowels compared to rounded vowels, and infants as young as 3 months of age associate rising pitch to more pointed shapes (see Section 10.5.2). These results suggest that sound/shape matching can influence vocabulary acquisition in toddlers. Indeed, in the only study to investigate this possibility directly, Japanese-learning 3-year-olds were better at generalizing the meaning of newly acquired verbs if they used sound symbolic mimetics than if they did not (Imai *et al.* 2008).

We cannot rule out an experiential explanation for sound-shape mappings in toddlers, as toddlers have had enough experience with words and the objects that they represent to pick up statistical regularities in English semantics. It is possible that words that have non-rounded vowels tend to represent objects that are jagged (e.g. spiky) and that words that have rounded vowels tend to represent objects with curved contours (e.g. round, amoeboid). Indeed, there are consistencies across languages in using words containing the non-rounded vowel i (as in feet) to name objects or attributes that are smaller, brighter, closer, and/or associated with higher pitch (e.g. tiny, mini) and in using words containing the non-rounded vowel o to name objects or attributes that are larger, darker, farther away, and/or associated with lower pitch (e.g. whopping; e.g. Day 2004; Nuckolls 1999; Tanz 1971). However, it is also possible that this effect represents a naturally-biased association between the shape and sound of the phoneme, between shape and the sight of the shape of the mouth when producing the sound, and/or between shape and the feeling (amount of oral constriction) needed to produce the same sound oneself. These natural associations may have influenced the evolution of language itself, as described above (Ramachandran and Hubbard 2001), and in turn they may influence the language learning of the individual child. Any or all of these associations could influence the language-learning child: young infants look preferentially toward a face with the lip movements matching the sound they are hearing or have just heard, initially even for foreign language contrasts (Pons *et al.* 2009; see Chapter 9 by Soto-Faraco *et al.*) and monkey calls (Lewkowicz and Ghazanfar 2006; see Chapter 7 by Lewkowicz and Chapter 16 by Ghazanfar), an effect that is modulated by the movements they are making with their own mouth (Yeung and Werker 2010; see Ito *et al.* 2009 for similar evidence from adults).

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10.6 Summary

In sum, development involves a proliferation of connections among and within sensory cortical areas followed by experience-dependent pruning that leads to more specialized sensory networks that are further enhanced by re-entrant feedback. When the pruning or inhibitory feedback are less-than-normal, some of the early crossmodal and cross-dimensional connections remain to influence conscious perception in the form of synaesthesia. In typical adults, remnants of these connections persist that directly influence associations and indirectly affect behaviour. During early childhood, however, these connections may have a stronger influence on the modalities and dimensions the child perceives as connected and on the words they find easy to learn. They will interact with the experience-dependent pruning driven by the child's individual environment to make some veridical associations easier to learn because the associations in the environment match the intrinsic connections in the young brain.

Thus the young infant appears to begin development with the neural substrate for both crossmodal and cross-dimensional synaesthetic associations, including both: (1) an equation of magnitude (e.g. louder = brighter, brighter = longer), and (2) a systematic linking between seemingly ↳ arbitrary attributes, the natural biases we referred to throughout this chapter. With development, some of these correspondences will be reinforced by experience and, when they are, it will lead to consolidation and refinement of the initial connections. These natural biases will influence the ease of the child's initial perceptual and language learning. At the same time, the child will learn other correspondences from regularities in the environment (e.g. this voice timbre goes with mother's face; mice make squeaky sounds; roses have a particular smell), likely in part by the interlinking of schemas as described by Piaget (1962). Natural biases that are not reinforced by correspondences in the child's environment will be largely pruned away, with the remainder likely inhibited by re-entrant feedback. Nevertheless, remnants of the natural biases will remain as unconscious influences on typical adult perception.

In those with synaesthesia, development takes a different course. Because of less-than-normal pruning and/or less than normal inhibition, more of the exuberant connections remain—especially among contiguous sensory cortical areas—as well as within the parietal cortex in areas binding stimulus properties together and within the frontal cortex. These connections include ones underlying the natural biases observed in early development and ones that are idiosyncratic, varying from individual to individual, but highly consistent over time. These connections are sufficiently strong and widespread to induce conscious synaesthetic percepts and accompanying cortical brain activity in the same areas activated by real world stimuli with the same attributes. Something similar may happen in the typical infant before experience-dependent pruning and the development of inhibition. Nevertheless, because many of the synaesthetic percepts link back to the initial natural biases, typical adults demonstrate crossmodal influences of similar type. For that reason, future research on synaesthesia has the potential to reveal other additional natural biases influencing the perception of all of us.

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