Reduced perceptual narrowing in synesthesia

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Synesthesia is a neurologic trait in which specific inducers, such as sounds, automatically elicit additional idiosyncratic percepts, such as color (thus “colored hearing”). One explanation for this trait—and the one tested here—is that synesthesia results from unusually weak pruning of cortical synaptic hyperconnectivity during early perceptual development. We tested the prediction from this hypothesis that synesthetes would be superior at making discriminations from nonnative categories that are normally weakened by experience-dependent pruning during a critical period early in development—namely, discrimination among nonnative phonemes (Hindi retroflex /d̪a/ and dental /ɖa/), among chimpanzee faces, and among inverted human faces. Like the superiority of 6-mo-old infants over older infants, the synesthetic groups were significantly better than control groups at making all the nonnative discriminations across five samples and three testing sites. The consistent superiority of the synesthetic groups in making discriminations that are normally eliminated during infancy suggests that residual cortical connectivity in synesthesia supports changes in perception that extend beyond the specific synesthetic percepts, consistent with the incomplete pruning hypothesis.

synesthesia | perceptual narrowing | speech perception | face processing | pruning

Synesthesia is a perceptual phenomenon in which a stimulus evokes not only the typical percept, but also an additional percept, often in another sensory modality (e.g., “colored hearing”). Its perceptual reality has been confirmed by evidence of long-term consistency and evidence that the extra percepts have predictable effects on behavior, such as inducing Stroop-like interference (1, 2). Moreover, the reported extra percepts co-occur with brain activation on fMRI scans in “appropriate” cortical areas (e.g., color induced by graphemes or sounds co-occurring with activity in area V4, the area activated in typical color processing) (3, 4). Estimates of the prevalence of synesthesia range from approximately 4% to 25%, depending on which types are included and the specific criteria used (5–9).

Although synesthesia runs in families, its developmental origins are unknown. One prominent hypothesis is that synesthesia occurs when the hyperconnectivity of cortical connections present in early development does not undergo the normal amount of experience-dependent pruning (3). In the typical infant, anatomic and imaging evidence point to such hyperconnectivity, which appears to be eliminated through pruning of connections that are rarely stimulated by environmental input (10). The hyperconnectivity supports synesthetic-like cross-modal influences on infants’ perception (11) and is hypothesized to be preserved to an unusual extent in adults with synesthesia. The main support comes from anatomic evidence of greater connectivity in and between appropriate areas of the brains of adult synesthetes compared to control adults (12–14; but see ref. 15). Converging evidence comes from increased correlations in thickness between distant cortical regions in adults with synesthesia (16), as well as the higher resting state connectivity that is widespread in and across hemispheres (17, 18). Instead, or in addition, the remaining connectivity in the cortices of adults with synesthesia may have greater functionality because of reduced inhibition (19, 20).

An alternative hypothesis is that synesthesia is the result of the learning of connections experienced during childhood, such as the color of letters on a set of refrigerator magnets or other childhood toys (21–23). Indeed, correlations of synesthetic percepts with the color of childhood toys/magnets have been documented in a minority of synesthetes, as have more general correlations with learning influences, such as letter frequency (8). Moreover, synesthetic-like phenomena can be induced by extensive training in typical adults (24, 25). Nevertheless, none of these findings means that such learning is sufficient, or even necessary, for the development of synesthesia, and provide no evidence against the incomplete pruning hypothesis.

Here we tested a prediction from the pruning hypothesis. In typical development, input during the first years of life tunes perception toward finer distinctions among items from native categories while diminishing discrimination for nonnative categories, a phenomenon termed perceptual narrowing. Perceptual narrowing is thought to result from pruning of the initial hyperconnectivity based on experience during infancy (10). This explanation is suggested by evidence from animal models that

Significance

The perceptual validity of synesthesia has been established by behavioral and neuroimaging evidence; however, its developmental origins remain unclear. Here we tested the hypothesis that synesthesia arises when there is less experience-dependent pruning during development. We did so by comparing adults with and without synesthesia on another phenomenon that results from experience-dependent pruning: perceptual narrowing of discrimination to native categories (native phonemes and upright human faces) to the detriment of non-native categories (non-native phonemes, chimp faces, and inverted human faces). Synesthetes were better than controls at all of the non-native discriminations, with no difference for the native categories. The results support the hypothesis that in synesthesia, there is decreased experience-dependent modification of the cortical hyperconnectivity present in early development.

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sensory cortical connections that are stimulated are strengthened and those rarely stimulated are pruned away (26), along with evidence that perceptual narrowing in human infants is experience-dependent—namely, that it can be prevented or reversed by the introduction of nonnative categories between 6 and 12 mo of age (27–30). It follows from the incomplete pruning hypothesis that adults with synesthesia will have undergone less perceptual narrowing and hence be better than typical adults at discriminating sensory stimuli from nonnative categories, even those unrelated to any form of their synesthesia. That is the hypothesis we tested here.

Specifically, we tested sensitivity to differences among nonnative phonemes and faces. The nonnative phoneme discrimination required hearing the difference between the Hindi retroflex /d̪a/ and dental /ɖa/, a discrimination demonstrated by 6- to 8-mo-old infants but thereafter only by speakers of a language in which, unlike English, it is phonemic—that is, used to contrast meaning between words (31, 32). Following an initial pretest, we attempted to improve performance by presenting a disproportionate number of trials with the more acoustically distinct instances of these phonemes, a training procedure known to be effective in improving nonnative discrimination in English-learning infants (33–35) and English-speaking adults (36, 37). Reduced perceptual narrowing in synesthesia might be manifested as superior performance on the pretest and/or increased learning after training.

The nonnative face sets comprised upright chimp faces and, for a subset of participants, inverted human faces. The task required matching a target face to one of two faces that differed only in the spacing of the internal features. Early in development, infants are as accurate at noticing changes in the identity of animal faces as of human faces (38, 39) and in the identity of inverted human faces as of upright human faces (40), but by adulthood that sensitivity diminishes relative to the improvement in the sensitivity for upright human faces, presumably as a result of the perceptual narrowing effected by experience-dependent pruning and attunement (38–41). Based on the hypothesized reduced experience-dependent pruning, we predicted that synesthetes would be more accurate than controls in discriminating among items from nonnative categories (i.e., foreign phonemes, chimpanzee faces, and inverted human faces).

We did not have an a priori prediction for native categories (familiar phonemes and upright human faces). In normal development, attunement to native categories co-occurs with decreased discrimination (tuning out) to nonnative categories (42), and this perceptual narrowing is posited to underlie the development of expertise (43, 44). However, the two might not be causally related, but each may result from separate processes of the reinforcement of stimulated neural connections and of the pruning of unstimulated connections. If they are causally related, then we would predict that decreased perceptual narrowing in synesthesia would co-occur with reduced expertise for native distinctions, that is, an interaction of group and stimulus in our experimental paradigm. On the other hand, if they are not causally related in normal development, then decreased pruning could leave nonnative discriminations intact while not degrading—and perhaps even enhancing—discrimination of native categories, that is, a main effect of group in our experimental paradigm.

The independence of experience-dependent strengthening (of stimulated synapses) and of experience-dependent pruning (of unused synapses) is evident in detailed studies of monocular deprivation in animal models; synapses connected to the deprived eye are eliminated before the expansion of synapses stimulated by the open eye (26). Similarly, the independence of tuning in to native categories and of tuning out of nonnative categories is evident in human adults labeled superrecognizers because of their extraordinary ability to recognize facial identity for native categories (e.g., adults, same race, upright). They are also superior at recognizing faces from rarely experienced categories, namely infants' faces (45) and other races' faces (46), with no correlation among these abilities.

To aid the interpretation of the findings from native and nonnative discrimination, in Experiment 1 we also included digit span as a control task in which we expected the synesthetes to have no or at most slight superiority (47). If synesthetes show an overall superiority in making both native and nonnative discriminations, the results for digit span will allow us to evaluate whether the differences might arise from higher overall motivation or attentiveness during the experimental session rather than from heightened perceptual sensitivity. In Experiments 1 and 2, we also included a variety of other tasks unrelated to perceptual narrowing to aid interpretation of the main findings.

Results

We used ANOVA to analyze the overall pattern of results and planned comparisons to test specifically whether synesthetes were more accurate than controls for nonnative categories, the conditions for which we had a prediction. The addition of white noise (*Materials and Methods*) made the phonetic distinctions of Experiment 1a difficult to hear for both groups, but the synesthetes were more accurate than the controls in discriminating the nonnative phonetic distinction (Fig. 1). ANOVA of the data from the pretest revealed a main effect of native/nonnative (native better), ($F_{(1,76)} = 8.523$, $P = 0.005$), no main effect of group (synesthete vs. control) ($F_{(1,76)} = 0.803$, $P = 0.37$), and a significant interaction between group and native/nonnative ($F_{(1,76)} = 4.310$, $P = 0.04$). As shown in Fig. 1, synesthetes were more accurate than controls in discriminating between nonnative sounds, but showed no such advantage for native discriminations. A planned comparison of the nonnative distinction confirmed that the synesthetes were more accurate during the pretest ($t_{(67)} = 2.07$, $P = 0.02$, Cohen's $d = 0.477$, one-tailed). Following the training period, performance improved for both groups (Fig. 1), although it remained superior for native discriminations (main effect of native/nonnative, $F_{(1,76)} = 934.01$, $P < 0.0001$). There was only a trend toward synesthetes to be more accurate than controls after training ($F_{(1,76)} = 3.618$, $P = 0.061$), with no significant interaction between group and native vs. nonnative ($F_{(1,76)} = 0.012$, $P = 0.91$). Analyses based on d-prime yielded the same pattern of results for the nonnative discriminations: for the pretest, the mean d-prime value for synesthetes was significantly larger than that for controls (1.59 vs. 0.39; $t_{(44)} = 4.26$, $P = 0.00005$, Cohen's $d = 1.01$, one-tailed), whereas after training, a trend remained for a larger mean for synesthetes compared with controls (1.04 vs. 0.73; $t_{(76)} = 1.47$, $P = 0.07$, Cohen's $d = 0.33$, one-tailed).

ANOVA on the data from Experiment 1b on the discrimination among human and chimp faces revealed a main effect of species (better accuracy for human faces) ($F_{(1,79)} = 109.541$, $P < 0.0001$), a main effect of group (synesthetes better) ($F_{(1,79)} = 4.997$, $P = 0.028$), and no interaction ($F_{(1,79)} = 1.354$, $P = 0.248$). A planned comparison revealed that, as predicted, synesthetes were more accurate than controls in discriminating among chimpanzee faces ($t_{(79)} = 2.700$, $P = 0.004$, Cohen's $d = 0.61$, one-tailed) (Fig. 2). These results were replicated in a sample tested 12 mo later with a longer exposure time (Experiment 2): a main effect of species ($F_{(1,57)} = 79.867$, $P < 0.0001$), a main effect of group ($F_{(1,57)} = 6.691$, $P = 0.012$), and no interaction ($F_{(1,57)} = 0.737$, $P = 0.394$). The planned comparison confirmed that accuracy for discriminating chimp faces was significantly better in synesthetes than in controls ($t_{(57)} = 2.467$, $P = 0.0085$, Cohen's $d = 0.64$, one-tailed). Reaction times on correct trials were faster for human faces ($F_{(1,57)} = 6.560$, $P = 0.013$), but there was no difference between groups ($F_{(1,57)} = 0.059$, $P = 0.808$), and no

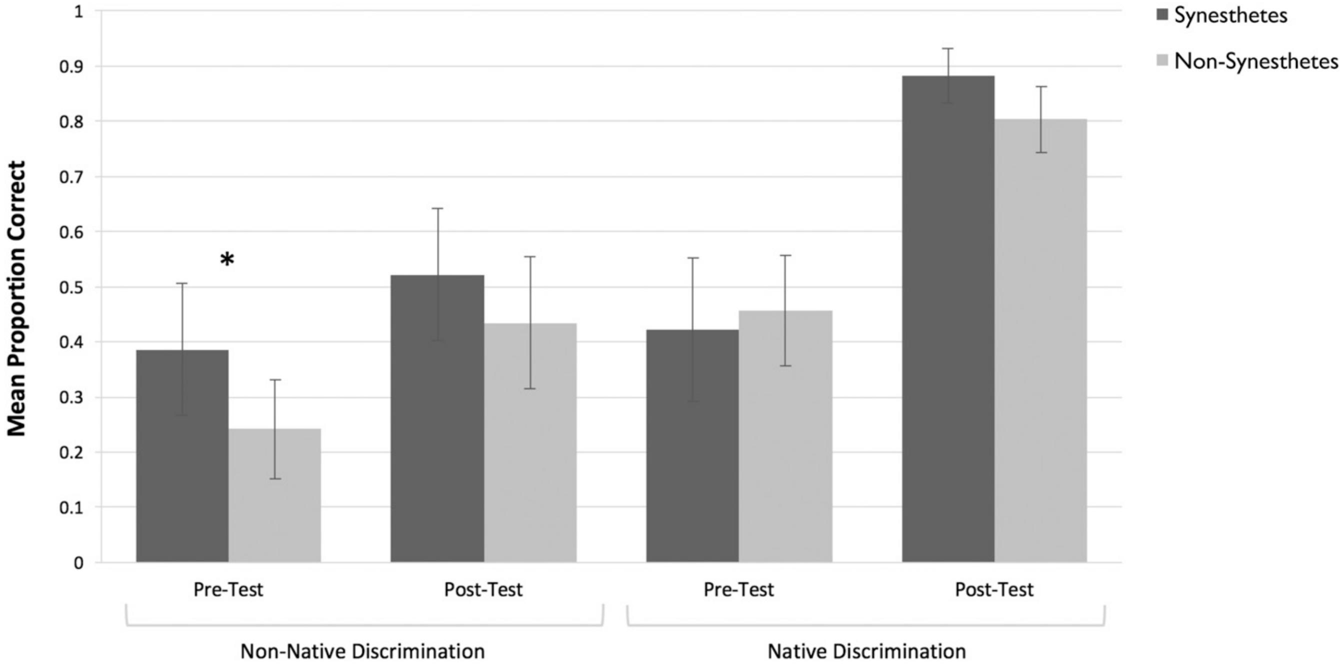

Fig. 1. Mean proportion correct (±95% confidence interval) for detecting phonetic differences during the pretest and the posttest of Experiment 1a. Shown is the accuracy on different trials. During the pretest, synesthetes (dark bars) were more accurate than nonsynesthetes (light bars) in making the nonnative distinctions (*Left*), with no such advantage for native differences (*Right*). The asterisk indicates a significant between-group difference for the nonnative comparison by planned one-tailed t tests: $^{*}P < 0.05$.

interaction ($F_{(1,57)} = 0.074$, $P = 0.787$). (Reaction times were not recorded accurately for Experiments 1a, 1b, and 1c.) For the subset of participants in the original sample tested with inverted human faces (Experiment 1c), as predicted, synesthetes were more accurate than controls when discriminating among inverted human faces ($t_{(36)} = 2.065$, $P = 0.0235$, Cohen's $d = 0.67$, one-tailed) (Fig. 2).

This superiority was replicated in reaction times in the sample tested with upright and inverted faces and longer exposure times 1 y later (Experiment 3): there was a main effect of orientation on accuracy ($F_{(1,38)} = 102.212$, $P < 0.0001$) and a trend for synesthetes to be more accurate ($F_{(1,38)} = 2.895$, $P = 0.097$), with no interaction ($F_{(1,38)} = 2.011$, $P = 0.164$). Synesthetes were quicker to make correct judgments ($F_{(1,38)} = 12.449$, $P = 0.001$ for group), with no effect of orientation ($F_{(1,38)} = 1.548$, $P = 0.221$) or interaction ($F_{(1,38)} = 0.048$, $P = 0.828$). Planned comparisons showed that synesthetes were more accurate than controls in discriminating spacing differences in the inverted block ($t_{(38)} = 2.055$, $P = 0.0235$, Cohen's $d = 0.65$, one-tailed), as well as faster than controls at making correct judgments about inverted faces ($P < 0.005$, Cohen's $d = 0.87$, one-tailed). The synesthetes did not differ from controls in digit span or any of the other control tasks (Table 1).

Discussion

As predicted, synesthetes were better at discriminating items from all three nonnative categories: a Hindi phonemic distinction, chimp faces, and inverted human faces. The effects were small but consistent across five experiments, presenting as an interaction between group and category for phonemes and as a main effect of group for faces, either on accuracy or on correct reaction times. In each case, the superiority for nonnative distinctions was confirmed by a planned comparison. These data provide evidence of less perceptual narrowing in synesthesia and, although indirect, behavioral evidence of incomplete pruning. They are consistent with evidence that the greater connectivity in the brains of adult synesthetes compared with control adults includes sensory areas that might be involved in face and phonemic discrimination, such as the fusiform gyrus, temporal cortex, and frontal cortex (3, 12–14, 48–50). Our findings suggest that the additional brain connectivity in synesthetic cortices supports not only specific synesthetic percepts, but also more generally enhanced perceptual abilities, including ones in domains that rarely lead to synesthesia, such as face perception. Such generally enhanced perceptual abilities are not predicted by the learning hypothesis. They are consistent with recent evidence of augmented sensory sensitivity and early visual sensory processing in adults with synesthesia, even in areas seemingly unrelated to any synesthetic experiences (6, 51–55, 55), of superior matching of facial identity by adults with colored-grapheme synesthesia (56), and of differences in intelligence and personality traits between adults with and without synesthesia (9).

Both behavioral perceptual narrowing and anatomic pruning are known to be experience-dependent and most plastic during a critical period early in development. For example, perceptual narrowing can be readily reversed by exposing infants nearing their first birthday to individual items from a nonnative category, be they chimp faces, other races' faces, chimp vocalizations, or musical rhythms (27–29, 31, 57). Similarly, abnormal pruning of connections following sensory deprivation occurs only early in life and can be reversed by early restoration of input (42, 58, 59). In both cases, experience of the same type later in life is ineffective. Thus, the evidence here of less perceptual narrowing in adults with synesthesia is consistent with the hypothesis of less experience-dependent pruning during a critical period early in life. However, as reviewed below, animal models suggest that incomplete pruning is not the sole possible explanation.

Animal models indicate that the onset of critical periods of experience-dependent plasticity is controlled by the maturation of particular inhibitory neurons (26), which balance the earlier formed excitatory circuits. Then the plastic process itself prunes less-used synapses to clear space for more salient connections to

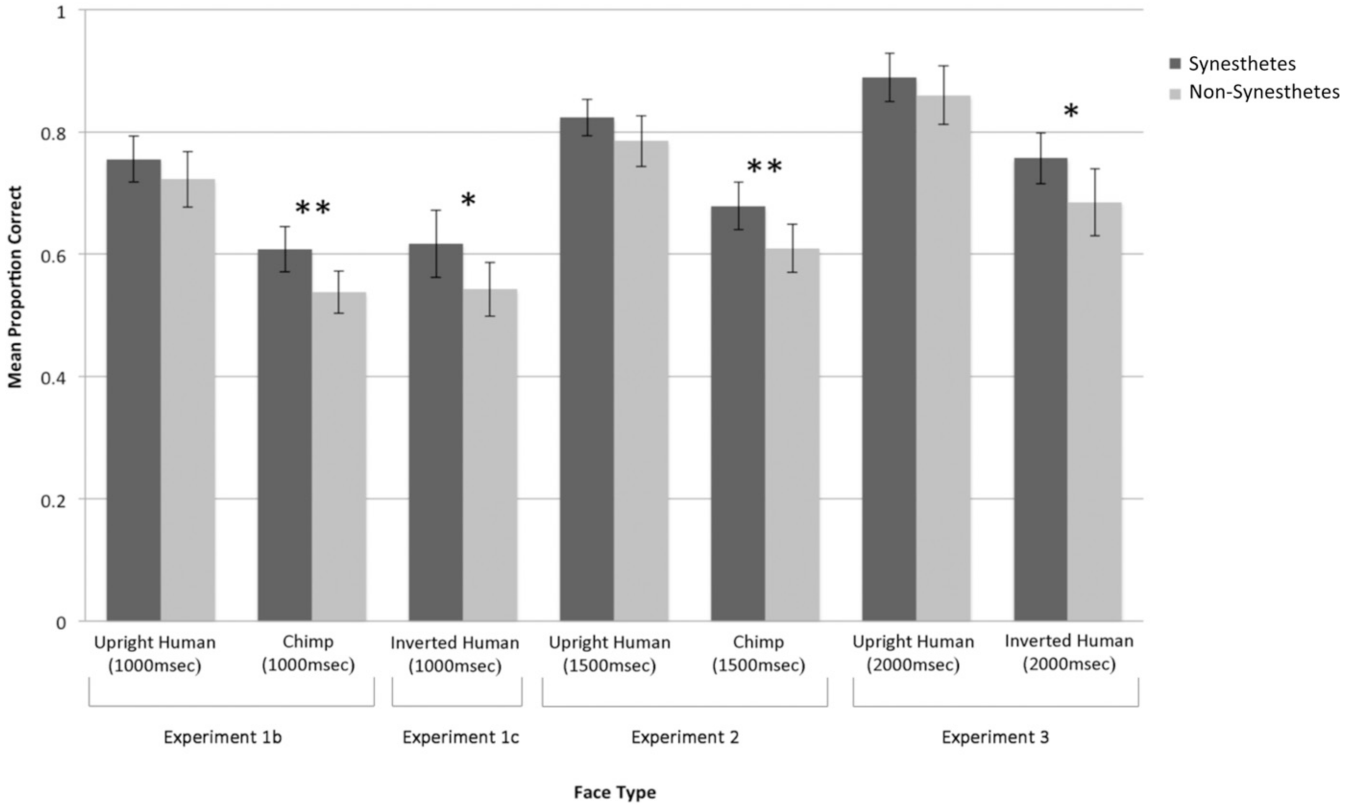

Fig. 2. Mean proportion correct (±95% confidence interval) for synesthetes (dark bars) and nonsynesthetic controls (light bars) for discrimination of upright human, chimpanzee, and inverted human faces. The three leftmost pairs of bars are from the original sample tested at 1,000 ms (Experiment 1b), including the inverted face data from a subsample (Experiment 1c). The other bars are from the replication samples tested with longer exposure times (Experiments 2 and 3). Asterisks indicate significant between-group differences for nonnative comparisons by planned one-tailed *t* tests: $^{*}P < 0.05$; $^{**}P < 0.01$.

sprout that reflect the sensory environment. Thus, the visual cortex becomes mainly responsive to light, the auditory cortex to sound, and so on. Under conditions of deprivation (60–64), ectopic sensory inputs may retain and strengthen their initial innervation of areas normally destined for a single modality. Ultimately, the sculpting process comes to an end and critical periods close when synapses mature and "brake-like" factors emerge to actively limit further plasticity (65). Thus, in addition to incomplete pruning, synesthetes might demonstrate less perceptual narrowing because of weaker suppression of latent intersensory connections, as postulated by the reduced inhibition hypothesis (19) and consistent with incomplete critical period closure (65). The differences in plasticity from incomplete pruning (or inhibition) may interact with the synesthete's environment to enhance particular connections, as evidenced by influences of letter frequency, position in the alphabet, exposure to a second language, color of refrigerator magnets, and other factors (8, 21–23, 66). However, the environmental correlations that influence synesthetic percepts can do so only because of the incomplete pruning evidenced by the literature and our present results.

By either explanation—incomplete pruning or reduced inhibition—less perceptual narrowing is not the result of learning environmental correlations. It is likely to arise from altered levels of plasticity and/or altered brakes on plasticity. This possibility is suggested by evidence from neuronal network models of developing perceptual sensitivity: heightened plasticity leads to capricious learning, which stabilizes as enhanced cross-talk between nodes, as is characteristic of synesthesia (67). Consistent with this view is evidence for genetic differences between synesthetic and nonsynesthetic adults related to alleles involved in brain connectivity and plasticity (68–70).

Synesthetes were not worse than controls in discriminating /ra/ from /la/ and in differentiating two upright human faces, and were superior overall in facial processing, much like the reported superiority of adult colored-grapheme synesthetes in recognizing

Table 1. Results of the control tasks

Task	Synesthete mean	Control mean	*t* test	Effect size (Cohen's *d*)	*P* value (one-tailed)
Total digit span	17.8	17.2	$t_{(73)} = 0.73$	0.15	0.23
Rey auditory-verbal memory test	11.6	11.5	$t_{(76)} = 0.20$	0.04	0.42
Face contour accuracy	0.88	0.87	$t_{(57)} = 0.56$	0.15	0.29
Face contour RT, ms*	616.6	605.3	$t_{(57)} = 0.34$	0.09	0.37
Face features accuracy	0.96	0.95	$t_{(54)} = 0.97$	0.25	0.17
Face features RT, ms	585.4	593.0	$t_{(57)} = 0.28$	0.07	0.39

*In this case, the synesthetic group was (nonsignificantly) slower than the control group.

facial identity and emotions (56). This pattern challenges current notions of the development of perceptual expertise and suggests that the improvements for native stimuli may occur independently of the decrements for nonnative stimuli. Such independence has been shown for superrecognizers, whose superiority for the native category (adult own race upright faces) co-occurs with superior processing of infants' faces (45) and other races' faces (46). In adults with synesthesia, connections underlying the discrimination of items from native categories might have been strengthened by the normal consolidation of experienced categories without the full complementary pruning of inexperienced ones. The remaining hyperconnectivity may also support the enhanced associative learning that has been documented in adults with synesthesia (71, 72).

Because the synesthete's superior performance for faces emerged as a main effect across native and nonnative categories, and not as an interaction (as it did for phonetic distinctions), a skeptic might argue that the synesthetes were generally more motivated or attentive than controls during the face tasks, leading to superior overall performance. However, we note that their advantage was primarily for nonnative categories (Figs. 1 and 2). More tellingly, the synesthetes did not differ from controls on other tasks included in the testing battery; specifically, the synesthetic group in Experiment 1 did not differ from controls on digit span or the Rey auditory verbal memory test. In Experiment 2, the synesthetic group did not differ from controls on face tasks with identical structure to the main task but based on cues (e.g., feature shape, external contour) unrelated to face expertise (73). Thus, their superiority was evident only for types of faces shaped by experience in typical development to favor native over nonnative categories.

Our conclusions are confounded by the fact that the categories of synesthesia represented in our sample were heterogeneous (*SI Appendix*, Table S1), ranging from common types, such as color induced by letters or pitches, to rarer types such as colored auras induced by different personalities. It included both "projectors" (with the extra percept projected in space) and "associators" (with the extra percept in "the mind's eye"), as well as synesthetes with only 1 to as many as 15 self-reported types of synesthesia. The effects that we observed here might have resulted primarily from only certain types of synesthesia and might not be a common characteristic of all forms.

Another limitation is that all the control subjects in the replication samples were naïve to the tasks, while some of the synesthetes had performed them before, roughly a year earlier. Therefore, the superior performance of synesthetes might represent a practice effect rather than a replication. However, we note that the same effects were found in Experiment 1, during which all participants were naïve, and that synesthetes in the replication samples were not better than controls for the native category (upright human faces; Fig. 2), even though that condition was also repeated, with accuracy not at ceiling. They were more accurate only for the nonnative categories (chimp and inverted human faces).*

In summary, this study presents evidence that compared with typical adults, synesthetes are able to more easily discriminate nonnative faces and phonemes. This pattern is qualitatively like that observed in infancy: young infants make these discriminations more readily than older infants. Thus, our results support the hypothesis that typical perceptual narrowing and the decrease in synesthetic-like perceptions in typical infants are mediated by the same developmental process, an experience-dependent process that does not play out fully in synesthesia.

Materials and Methods

Participants. Synesthesia (or lack thereof) was verified using an online standardized battery of tests (74). The tests begin by asking about the experience of specific forms of synesthesia, followed by tests of the consistency for the reported forms, during which participants choose the percept (e.g., color) associated with each of their synesthetic inducers (e.g., letters) three times.

Our study adopted a recent criterion of genuineness, in which the mean sum of the pairwise Euclidean distances between each of the three colors chosen for an inducer must be less than 135 CIELUV units for the participant to qualify as synesthetic (75). For forms of synesthesia not tested by the battery (e.g., personality → color or aura), an experimenter checked consistency by questioning the participant about the specific induced percepts on two separate occasions.

For the main experiments (Experiments 1a and b), synesthesia was verified in 38 participants by the Eagleman battery (74), and in an additional three by the interviews, for a total sample of 41 synesthetes (26 females). They ranged in age from 17 to 43 y (mean age, 22.8 y). All but six were undergraduate students (three had completed or were completing, high school; three had completed their undergraduate degrees). An additional five self-reported synesthetes were excluded because their synesthesia could not be verified. *SI Appendix*, Table S1 provides details on the types of synesthesia in the included participants. A total of 59 controls age 18 to 24 y without synesthesia were tested, but the control group for the studies of phoneme and face discrimination were not identical, because we eliminated those with fluency in a relevant South Asian language for the phoneme study and attempt to matched ethnicity for the face studies. All but one were pursuing an undergraduate degree; one had completed that degree. The gender of one synesthete and the age of five participants (two synesthetes and three controls) are missing; these participants were included only in the auditory tasks.

Participants were recruited and tested at McMaster University, the University of British Columbia, and Simon Fraser University. The experiments were approved by the Institutional Ethics Review Boards of all three universities. Participants were recruited via websites describing psychology experiments, via posted flyers, and as part of a large-scale survey of synesthesia (8). They received course credit and/or financial compensation for participation. All participants gave informed consent after the procedures were explained. All reported normal hearing, and all passed a vision screening test that included tests of monocular acuity and stereopsis.

Auditory Tasks: Experiment 1a.

Participants. All participants were tested in Experiment 1a, but data are limited to those of 34 synesthetes (mean age, 23.5 y; range, 17 to 43 y; 23 females, 10 males) and 44 controls (mean age, 19.8 y; range, 18 to 24 y; 35 females), because of the exclusion of those who speak a South Asian language in which the nonnative contrast may be phonemic. Gender was not recorded for one synesthete; age was not revealed by five participants (three synesthetes and two controls).

Stimuli. Stimuli were synthesized speech sounds lasting 275 ms, generated at steps 1, 3, 6, and 8 along an eight-step continuum (31, 34) ranging between the Hindi retroflex /d̪a/ and dental /ɖa/ (nonnative) or between /ra/ and /la/ (native). Because pilot participants performed at ceiling on some pairings, the difficulty of the task was increased by masking the sounds with white noise at a signal-to-noise ratio of 25 dB. Each trial contained a pair of sounds—either identical (a pair of 3–3 or 6–6 phonemes) or different (1-8 or 8–1). In addition, to increase difficulty for the native pair, we included similar pairings (1-2, 2-1, 7-8, or 8–7).

Procedure. The procedure began with the discrimination task. Each trial consisted of a pair of sounds, each presented for 300 ms separated by 1,000 ms. A response cue appeared at 1,000 ms after the start of the second sound. Once the subject indicated whether the two sounds were the same or different, the next trial began without feedback. Each pairing was presented four times, except for the native similar pairs, which were presented twice each. Order was semirandomized across participants, the only constraint being that no pairing appeared consecutively more than twice.

After the discrimination task, participants received exposure training. They passively watched a 186-s video of moving colored dots forming flower shapes (to hold their attention), while all eight sounds from both the native and nonnative continua were played in a pseudorandom order in six blocks of 24 tokens each. Nonnative sounds were bimodally distributed such that tokens in positions 2 and 7 were played four times more frequently and

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*For Experiment 2, the results were similar when restricted to the 20 naïve synesthetes and 31 controls: synesthetes were more accurate than controls at discriminating monkey faces (0.67 vs. 0.61; $t_{(46)} = 2.158$, $P = 0.018$, Cohen's $d = 0.605$, one-tailed test). There was an insufficient number of naïve synesthetes to conduct a similar analysis for Experiment 3.

tokens in positions 3 and 6 were played two times more frequently than the single presentation of tokens in positions 1, 4, 5, and 8. This distribution has been shown to facilitate learning to hear the discrimination of retroflex and dental phonemes, even in adults (36, 37). Native sounds were equally likely from all eight positions. Each phoneme was followed by a 1,000-ms interstimulus interval. Subjects were instructed to watch the screen and concentrate on the sounds. Following the exposure video, participants repeated the discrimination task.

For Experiments 1a, 1b, and 1c, reaction time data were not analyzed because participants were not instructed to keep their hands on the keyboard between trials.

Faces Tasks.

Participants. For the face tasks of Experiment 1b, the final sample consisted of 41 confirmed synesthetes and 40 of the 59 control participants (mean age, 19.6 y; 31 females). The controls were selected so as to reduce differences in ethnicity between the two groups to avoid an unequal "other race" effect—the known superiority in discriminating faces from one's own ethnic group (44). In the synesthetic group, 30 self-identified as Caucasian and 11 as Asian; in the control group, 20 self-identified as Caucasian and 20 as Asian. A subset of the sample (those tested at McMaster University) participated in Experiment 1c by performing an additional block with inverted human faces. This subset included 19 synesthetes (mean age, 21.8 y; 12 females) and 19 controls (mean age, 19.7 y; 14 females). In both groups, 13 reported their ethnicity as Caucasian and 6 as Asian.

One year later, for Experiment 2, a replication sample of 28 synesthetes, comprising 20 new participants and 8 participants from the original sample of Experiment 1b, were tested with human and chimp faces using the same procedure, except that 1) the presentation time was increased from 1,000 ms to 1,500 ms so as to improve overall accuracy; 2) a different human model was used to make the human spacing set; 3) participants were told to keep both hands on the keyboard at all times, to provide a reliable measure of reaction time; and 4) all participants were Caucasian, with the exception of two synesthetes who reported their ethnicity as Asian. The results for these 28 synesthetes (mean age, 22.25 y; 19 females) were compared with those for 31 new controls (mean age, 20.3 y; 22 females) without synesthesia. This group was also tested with monkey and sheep faces, but ceiling (monkey: >85% accuracy by the control group, better than for upright human faces) and floor (sheep: <60% accuracy by the control groups, only slightly above chance) effects prevented meaningful comparison of the two groups. We suspect that these effects arose because differences in head size made the spacing differences more (monkey) or less (sheep) prominent, since the magnitude of spacing manipulations was kept constant in physical size rather than as a proportion of head circumference.

At a later point in the second year, for Experiment 3, a sample of 20 synesthetes (5 from the original sample in Experiment 1c and 15 additional synesthetes) performed the upright and inverted human spacing blocks with exposure time increased to 2,000 ms to facilitate performance in the inverted block. All but one of the synesthetes had participated in Experiment 2. As in Experiment 2, they were instructed to keep their hands on the keyboard so that we could collect accurate reaction times. The results of these 20 synesthetes (mean age, 22.6 y; 12 females) were compared with those of 20 novice controls without synesthesia (mean age, 20.1 y; 14 females). All participants in both samples reported their ethnicity as Caucasian. This subsample was also tested with four blocks of faces filtered to remove specific ranges of spatial frequency. The order of trial blocks was counterbalanced. The filtered blocks will be reported in detail elsewhere.

Apparatus and stimuli. The visual tasks were programmed in SuperLab 4.0 running on a Macintosh OSX 10.4.2 computer. Stimuli were presented on a Dell Trinitron 50-cm monitor with a resolution of 1,280 × 960 and a refresh rate of 85 Hz.

Three types of face stimuli were presented: upright chimpanzee faces, upright human faces, and inverted human faces. Faces in all three categories were cropped to remove backgrounds and hair, then transformed to greyscale and resized so that each face was 10.2 cm wide × 15.2 cm high. Upright human face stimuli consisted of nine faces (one original and eight morphed) and were identical to those used previously (76) (Fig. 3*A*). The original face (i.e., "Jane") was of an adult Caucasian female with a neutral expression. Eight morphed faces (i.e., "Jane's sisters") were created using Adobe Photoshop CS3 by manipulating the distance of spacing among facial features—that is, the eyes were moved upward or downward or toward or away from the nose by 4 mm, and the mouth was moved either up or down by 2 mm (Fig. 3*A*). Those faces presented in the inverted human faces block consisted of the same nine faces as in the upright condition but inverted 180° (Fig. 3*B*).

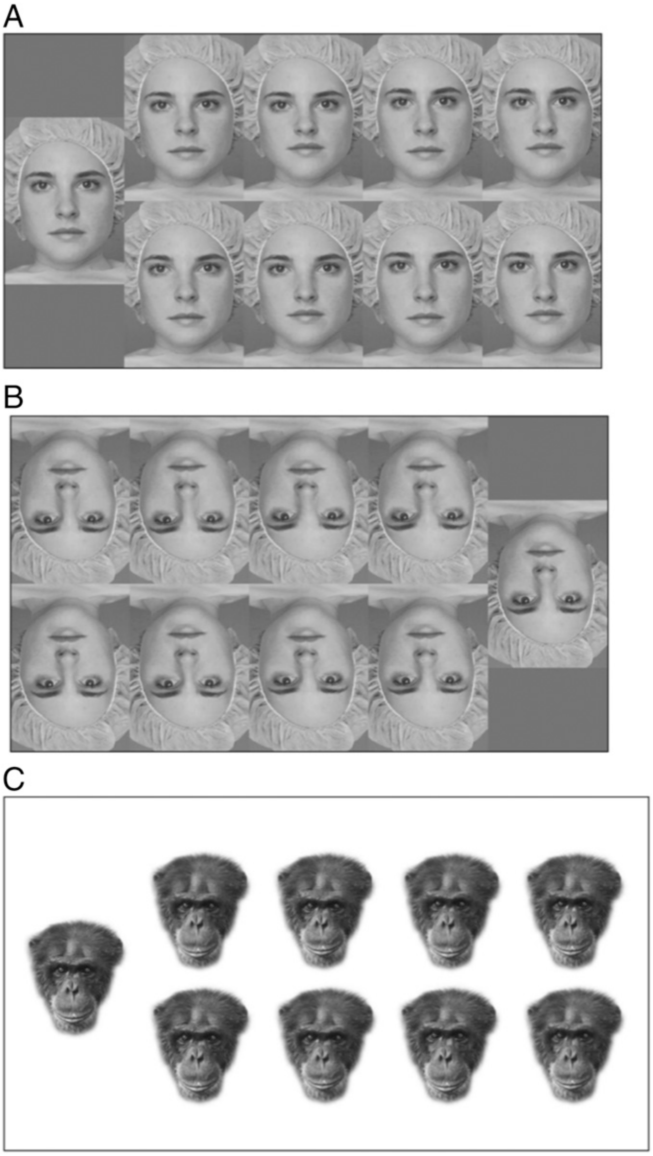

Fig. 3. The original (the single image) and two rows of morphed "sisters" used in the upright human (*A*), inverted human (*B*), and chimpanzee face (*C*) discrimination tasks.

Chimpanzee face stimuli were created in a similar manner. An original face (i.e., "Chimpanzee Jane"), chosen from a sample of colored, full-body chimp photos provided by Lisa Parr at the Yerkes National Primate Research Center in Atlanta was resized, converted to greyscale, and then modified with Adobe Photoshop CS3 to create eight additional chimpanzee faces (i.e., "Chimpanzee Jane's sisters"). Feature spacing modifications for the chimpanzee faces were identical to those performed on the human faces (Fig. 3*C*).

At the testing distance of 100 cm, the distance that the eyes and mouths moved with the spacing modifications corresponded to visual angles of 0.23° and 0.12°, respectively. Each image subtended a visual angle of 5.7° (height) × 9.1° (width) on the screen. Stimuli were presented on a white background with a luminance of 20.4 cycles/degree.

Procedure. Participants were seated in a dimly lit room at a viewing distance of 100 cm from the computer screen. The order of trial blocks (upright human, upright chimp, inverted human) was counterbalanced across participants. Each block began with a brief description of the task, including an introduction to "Jane" (human, chimpanzee, or inverted) and her eight "sisters." In each trial, three faces were presented simultaneously on the screen for 1,000 ms in Experiments 1b and 1c: one target face centered at the top of the screen and two test faces in the opposite bottom corners (one of which was identical to the target face). A noise mask was then presented for 250 ms, after which a response screen (a question mark) prompted participants to indicate, via a left or right key press, which test face matched the target face.

For each block, participants completed four practice trials before the test trials. For each face type, each of the nine faces was presented four times, for a total of 36 trials per block. Target face presentation order was randomized within each block, and location of the correct test face was counterbalanced. Participants took approximately 5 min to complete each individual trial block. All participants at McMaster, Simon Fraser, and University of British Columbia completed the upright human and chimp blocks. Participants at McMaster also completed the inverted human face block (Experiment 1c). The procedure was the same in the replication samples of Experiments 2 and 3 except for the increase in exposure time noted under Participants and the change in instructions to allow the collection of reaction times, in addition to accuracy.

Control tasks. Participants in Experiment 1 completed a standard test of forward and backward digit span, and the Rey auditory verbal memory. Data are missing for 4 of the 41 synesthetes and 1 (digit span) or 2 (verbal memory) of the 59 controls. Participants in Experiment 2 completed two additional tests of face perception using measures that do not underlie adult expertise: sensitivity to the shape of facial features and to the shape of the external face contour in upright human faces (77). Both followed the same format as the tests with human and chimp faces differing in the spacing of features.

Analyses. Because we predicted that synesthetes would be more accurate (or faster) than controls for nonnative distinctions but had no prediction for native distinctions, we tested for differences by conducting, for each sample, ANOVA with group as a between-subject factor and stimuli as a within-subject factor. Support for the prediction would appear as a main effect of group or an interaction of group and stimuli. ANOVA was followed by planned comparisons between groups for the nonnative distinction using independent-samples t tests, with the one-tailed prediction that synesthetes would be more accurate (or faster) than controls. For these analyses, we assumed unequal variance. The α level was set at 0.05. For the control tasks, we used t tests to compare the two groups because there was no within-subject variable.

Materials and Data Availability. All materials and data discussed in the paper are available on request to the corresponding author. They have not been deposited in an open access depository because of the complexity of three interinstitutional agreements and the possible identifiability of some of the synesthetic participants. Identity will be disguised before fulfilling any data request.

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