What does a neuron learn from multisensory experience?

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The brain uses different sensory inputs synergistically to maximize the detection and identification of environmental events (Stein and Meredith 1993). This fundamental capacity for multisensory integration is critical for survival, but is neither inborn nor predetermined and, as shown by studies of multisensory neurons in the superior colliculus (SC), is acquired only after extensive postnatal experience with cross-modal cues. Only then can cross-modal inputs be integrated to enhance the responses of SC neurons and the detection and orientation behaviors that depend on them (Stein 2012).

However, the nature of the maturational change that takes place in these neurons is not yet clear. One assumption is that once a neuron has had sufficient experience to develop the underlying neural mechanisms required for multisensory integration, it is able to integrate any of the cross-modal inputs to which it is responsive (Wallace et al. 2004). In short, its general integrative capability has matured. Two complementary observations support the view. First, that SC neurons trained to integrate a single pair of cross-modal inputs (i.e., visual-auditory) are capable of integrating them even when the physical features of the visual and auditory stimuli are substantially altered (Xu et al. 2012), and second, that early deprivation in one sensory modality not only affects multisensory integration involving that modality, but also the integration taking place among other modalities (Hotting et al. 2004; Occelli et al. 2012; Wallace et al. 2004).

Nevertheless, explicit proof for this hypothesis has not yet been provided. The alternative possibility, that neurons do not develop a general integrative capability, but one specific to each cross-modal pairing, cannot yet be excluded. Although this alternative would involve a more nuanced experiential process, and greater sophistication in the learning rules operating at the level of the individual multisensory neuron, it is no less possible. Distinguishing between these alternatives would be straightforward if, for example, obtaining the cross-modal experience with visual and auditory cues necessary for a trisensory (visual-auditory-somatosensory) SC neuron to integrate visual and auditory inputs could be shown to be sufficient for it to integrate auditory and somatosensory cues and vice versa. The present experiments directly examined this issue by rearing animals in environments that compromised either visual or auditory experience and then examining the ability of trisensory (as well as bisensory) SC neurons to integrate the different cross-modal stimulus pairs to which they were responsive. The results indicate that SC neurons do not incorporate a general integrative rule, but instead must learn each pairwise cross-modal association independently.

MATERIALS AND METHODS

All experimental protocols complied with the National Institutes of Health Guide for the Care and Use of Laboratory Animals, 8th Ed. (NRC 2011), and were approved by the Animal Care and Use Committee of Wake Forest School of Medicine, an Association for the Assessment and Accreditation of Laboratory Animal Care International-accredited institution.

Experimental Groups

A total of nine cats (six males and three females) were used: three were reared in standard housing conditions, three were reared in a dark room from birth, and three were raised from birth in a room with continuous 80-dB omnidirectional broadband noise provided by speakers (n = 5) located on all sides of their pen. Daily care observations and routine veterinary procedures for dark-reared animals were conducted using infrared goggles and an infrared viewing system that was activated periodically to allow the animals to be monitored from an adjacent room. In all other relevant respects, the housing and care provided was the same for all animals.

Efforts were made to preclude any confounding visual and auditory experiences in the dark-reared and noise-reared groups by anesthetizing animals in their home cages and maintaining anesthesia throughout experimentation. Thus, care was taken to minimize the exposure of animals to restricted modalities. Despite these efforts, however, no sensory restriction paradigm can be absolute and simultaneously allow evaluation of those senses. Minimal cross-modal experience can be acquired by animals during electrophysiological testing, albeit no
experimentially-induced effects were noted over the comparatively short series of recording experiments. In the case of noise-reared animals, some patterned auditory stimuli were expected to evoke masking by the omnidirectional noise stimulus. Noise-reared and dark-reared cats began recording sessions at 12–14 mo of age, and had 9–12 and 8–15 recording experiments respectively in both SCs.

Implantation Surgery and Electrophysiological Recording

Animals were anesthetized with ketamine hydrochloride (20 mg/kg im) and acepromazine maleate (0.1 mg/kg im), intubated through the mouth, and then placed in a stereotaxic apparatus. Isoflurane anesthesia (2–4%) was then induced and maintained (1.5–2%) during surgery. Expiratory CO₂, blood pressure, and heart rate were continuously monitored using a digital vital signs monitor (VetSpecs VSM7), and body temperature was maintained at ~37–38°C with a heating pad. A recording chamber that provided access to the SC was placed over a craniotomy and attached to the skull with screws and dental acrylic. Dexamethasone sodium phosphate was administered prior to surgery (1 mg/kg im, once daily, 1 day prior to surgery; once daily perisurgery) and after surgery (0.5 mg/kg im, twice daily for 3 days postsurgery; 0.25 mg/kg im, twice daily on postsurgery day 4; once daily on postsurgery day 5) to reduce the likelihood of brain edema. After surgery, analgesic (buprenorphine 0.005–0.01 mg/kg im) was administered twice daily for 3 days. In addition, antibiotic (ceftriaxone, 20 mg/kg im) was administered twice daily for 7 days.

After a postsurgical recovery period of at least 7 days, weekly recording began. The animal was anesthetized with ketamine hydrochloride (20 mg/kg im) and acepromazine maleate (0.1 mg/kg im), intubated, and artificially respired. Paralysis was induced with an injection of pancuronium bromide (0.1 mg/kg iv) to prevent ocular drift. Anesthesia, paralysis, and hydration were maintained by continuous intravenous infusion of ketamine hydrochloride (5–10 mg·kg⁻¹·h⁻¹), pancuronium bromide (0.05 mg·kg⁻¹·h⁻¹), and 5% dextrose in sterile saline (2.4–3.6 ml/h). Body temperature was kept at 37–38°C. Respiratory rate and volume were adjusted to keep the end-tidal CO₂ at ~4.0%. Expiratory CO₂, heart rate, and blood pressure were monitored continuously, and drug administration adjustments were made as necessary to maintain anesthesia.

Conventional methods were used for single-neuron electrophysiological recording as reported in the past (Xu et al. 2012). A glass-coated tungsten electrode (tip diameter: 1–3 μm, impedance: 1–3 MΩ at 1 kHz) was advanced through the multisensory (i.e., deeper) layers of the SC using a hydraulic microdrive to search for single neurons. An isolated single neuron was identified using a threshold criterion of three times the elevation of the action potential amplitude above background noise. The neural activity was recorded and amplified and routed to an oscilloscope, audio monitor, and computer for online and offline analyses. At the end of the recording session, saline (40–50 ml) was given subcutaneously as needed, and anesthetic and paralytic agents were discontinued. Once stable respiration and locomotion returned, the animal was returned to its home cage.

Sensory-responsive neurons were identified using a variety of visual, auditory and somatosensory search stimuli. Visual search stimuli consisted of moving or flashed bars of light back-projected from an LC 4445 Philips projector onto a tangent screen placed in front of the animal. Auditory search stimuli consisted of broadband (20–20,000 Hz) noise bursts and tones delivered from speakers placed around the animal and manually produced sounds. Somatosensory search stimuli consisted of taps, brushes, and manual manipulation of deep tissue and movement of joints. Whenever a multisensory neuron was identified, its receptive fields were mapped using conventional methods (Xu et al. 2012). Visual, auditory and somatosensory receptive fields were transferred to standardized representations of visual-auditory space and a diagram of the body surface (Stein and Meredith 1993).

To maximize the sample of trisensory neurons, each neuron encountered was subjected to an extensive battery of tests with the three types of stimuli interleaved to determine its modality-convergence pattern (i.e., trisensory, bisensory, unisensory). Once this pattern was determined, each multisensory neuron’s unisensory and multisensory responses were quantified using randomly interleaved modality-specific and cross-modal stimulus pairs at intertrial intervals of 5–7 s. Generally, this involved interleaving stimuli from each cross-modal stimulus pair and their component stimuli (3 sequences of 3 conditions).

In some cases, all combinations involving a visual stimulus were combined into a single interleaved sequence (5 conditions: visual, auditory, somatosensory, visual-auditory, visual-somatosensory) before running the auditory-somatosensory sequence (3 conditions: auditory, somatosensory, auditory-somatosensory). Visual stimuli (100- to 200-ms duration) were rectangular bars of light (6° x 2°) of varying intensity (1.1–13.5 cd/m² against a 0.86 cd/m² background) and moved in the optimal direction and speed. The auditory stimulus consisted of brief (100–200 ms) broadband noise bursts (20–20,000 Hz) of varying intensity (55–70 dB sound pressure level against an ambient background of 51.4–52.7 dB sound pressure level), originating from any of 15 hoop-mounted speakers placed 15° around the animal and manually produced sounds. Sensory-responsive neurons were identified using a variety of visual, auditory and somatosensory search stimuli. Visual search stimuli consisted of moving or flashed bars of light back-projected from an LC 4445 Philips projector onto a tangent screen placed in front of the animal. Auditory search stimuli consisted of broadband (20–20,000 Hz) noise bursts and tones delivered from speakers placed around the animal and manually produced sounds. Somatosensory search stimuli consisted of taps, brushes, and manual manipulation of deep tissue and movement of joints. Whenever a multisensory neuron was identified, its receptive fields were mapped using conventional methods (Xu et al. 2012). Visual, auditory and somatosensory receptive fields were transferred to standardized representations of visual-auditory space and a diagram of the body surface (Stein and Meredith 1993).

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| Table 1. Trisensory neurons: incidence and magnitude of multisensory integration |
|---------------------------------|-----------|----------------|---------------|----------------|
|                                | VA        | VS             | AS            |
|                                | Integration | Nonintegration | Integration | Nonintegration |
| Control                        |           |                |               |                |
| Incidence                      | 84 (47/56) | 16 (9/56)      | 77 (43/56)    | 23 (13/56)     |
| ME                             | 104 ± 7   | 24 ± 7         | 88 ± 6        | 24 ± 6         |
| Mean ME                        | 91 ± 7    | 73 ± 6         | 106 ± 7       | 16 ± 6         |
| Dark-reared                    |           |                |               |                |
| Incidence                      | 17 (8/47) | 83 (39/47)     | 11 (5/47)     | 89 (42/47)     |
| ME                             | 87 ± 11   | 6 ± 4          | 90 ± 16       | 8 ± 4          |
| Mean ME                        | 20 ± 5    | 17 ± 5         | 104 ± 8       | 14 ± 9         |
| Noise-reared                   |           |                |               |                |
| Incidence                      | 22 (11/51)| 78 (40/51)     | 75 (38/51)    | 25 (13/51)     |
| ME                             | 85 ± 8    | 11 ± 5         | 117 ± 9       | 15 ± 6         |
| Mean ME                        | 27 ± 6    | 91 ± 9         | 94 ± 9        | 3 ± 4          |

Incidence: percentage of neurons showing multisensory enhancement, which is defined as a significant increase in the number of impulses to the combined cross-modal stimuli compared with the most effective single-modality stimulus (t-test, P < 0.05). ME, the magnitude of multisensory enhancement. ME = [(CM – SMmax)/SMmax] × 100, where CM represents the mean magnitude of the multisensory response and SMmax represents the magnitude of the response evoked by the more effective modality-specific stimulus. VA, visual-auditory; VS, visual-somatosensory; AS, auditory-somatosensory.
of the probe could be varied independently. Stimulus intensities were adjusted to evoke weak unisensory responses (consisting of few impulses) in each neuron independently to maximize the amplitude of multisensory enhancement (ME) according to the “principle of inverse effectiveness” (Meredith and Stein 1986) in each neuron of each group.

Impulse times (1-ms resolution) were recorded for each trial and analyzed offline. The response window was defined for each neuron in the same way by using a geometric algorithm based on the cumulative impulse count described in an earlier study (Rowland et al. 2007). The magnitude of each response was identified as the mean number of impulses occurring in the response window minus the expected number given the spontaneous firing rate (mean spontaneous firing rate for each condition was calculated in the 500-ms window preceding the stimulus). The response to the combined cross-modal stimuli was statistically compared with the response evoked by the more effective modality-specific stimulus (t-test, \( P < 0.05 \)). Multisensory enhancement was defined as a significant increase in the number of impulses to the combined cross-modal stimuli compared with the most effective single-modality stimulus. The magnitude of this multisensory response enhancement was evaluated with ME: ME = \([CM - SM_{max}] / SM_{max} \times 100\), where CM represents the mean magnitude of the multisensory response, and SM_{max} represents the magnitude of the response evoked by the more effective modality-specific stimulus (Meredith and Stein 1983).

Data were compared statistically to determine significant differences. Incidence values were compared across groups using \( \chi^2 \) tests; ME values were compared using t-tests, Mann-Whitney rank sum tests; and ANOVA was used to evaluate trends where more than three groups were involved.

RESULTS

Three groups of cats (\( n = 3 \) in each) were used in the present experiments: a normal “control” group, a “dark-reared” group reared without light exposure, and a “noise-reared” group reared with omnidirectional sound (see MATERIALS AND METHODS). A total of 562 SC neurons (154 trisensory and 408 bisensory) were recorded in these animals (see Tables 1 and 2), with all experimental groups exhibiting all possible modality convergence patterns (Fig. 1). However, because trisensory neurons were expressly sought in each animal and in each condition by testing each neuron encountered in each electrode penetration with stimuli in all three modalities individually and in combination, their incidence, shown in Table 1, proved to be higher than previously reported (Kadunce et al. 2001; Meredith and Stein 1986). A neuron’s integration of concordant cross-modal signals was indicated by a significantly more robust multisensory response than the response to either component stimulus (Stein et al. 2009). The incidence of neurons showing elevated multisensory responses for each stimulus combination, and the mean proportional multisensory response enhancement (or ME, a measure of the effectiveness of multisensory integration), were calculated for each population and cross-modal pairing. There were no reliable differences in the observed pattern of results across animals within experimental groups or across experimental sessions. There were no significant differences in the visual and auditory stimulus intensities used for testing neurons’ ME capabilities in the three groups (Kruskal Wallis test, auditory stimulus: \( P = 0.25 \); visual stimulus: \( P = 0.718 \)).

Trisensory Neurons

Trisensory neurons in the control group displayed an equal likelihood (\( P = 0.605, \chi^2 \) test) of integrating each of the different cross-modal stimulus pairs (Table 1). Furthermore, ME (see MATERIALS AND METHODS) showed no significant variation across

![Fig. 1. The convergence patterns of superior colliculus (SC) neurons studied in each rearing condition. The neuronal population in control, dark-reared and noise-reared animals had all possible convergence patterns among the three senses represented in the SC. However, there was a small but statistically significant decrease in the incidence of visually-responsive neurons in dark-reared animals, and a corresponding change in the incidence of auditory-responsive neurons in noise-reared animals. VA, visual-auditory; VS, visual-somatosensory; AS, auditory-somatosensory; VAS, visual-auditory-somatosensory.](http://jn.physiology.org/)

Table 2. Bisensory neurons: incidence and magnitude of multisensory integration

<table>
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<tr>
<th></th>
<th>VA</th>
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<th>VS</th>
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**Table 2. Bisensory neurons: incidence and magnitude of multisensory integration**

- VA: Visual-Auditory
- VS: Visual-Somatosensory
- AS: Auditory-Somatosensory
- VAS: Visual-Auditory-Somatosensory

**VA**

**Nonintegration**

- Control
  - Incidence: 77 (58/75)
  - ME: 98 ± 6
- Dark-reared
  - Incidence: 10 (7/73)
  - ME: 58 ± 10
- Noise-reared
  - Incidence: 19 (14/74)
  - ME: 84 ± 9

**VS**

**Nonintegration**

- Control
  - Incidence: 71 (29/41)
  - ME: 91 ± 9
- Dark-reared
  - Incidence: 14 (4/28)
  - ME: 60 ± 12
- Noise-reared
  - Incidence: 74 (29/39)
  - ME: 117 ± 11

**AS**

**Nonintegration**

- Control
  - Incidence: 87 (26/30)
  - ME: 72 ± 8
- Dark-reared
  - Incidence: 62 (18/25)
  - ME: 100 ± 12
- Noise-reared
  - Incidence: 72 (22/23)
  - ME: 76 ± 9
the pairs ($P = 0.138$, one-way analysis of variance, range: 73–91%). A typical trisensory neuron is illustrated in Fig. 2A.

**Dark-reared group.** Although the visual receptive fields of dark-reared neurons were larger and had poorer spatial fidelity than normal (Wallace et al. 2004; Yu et al. 2010), many of them integrated auditory-somatosensory cues (77%, 36/47; $P = 0.652$) with normal ME levels ($P = 0.54$, t-tests see Table 1 and Fig. 2B). In short, there was no apparent rearing effect on

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**Fig. 2.** The development of multisensory integration capabilities in trisensory SC neurons following different rearing conditions. **A:** multisensory enhancement in a normal trisensory neuron was produced by any cross-modal stimulus combination. **Left:** the sensory convergence pattern. **Middle:** rasters (ordered bottom to top) illustrate responses to the 3 modality-specific and 3 cross-modal stimuli. **Right:** the summary bar graph illustrates the mean responses elicited by each stimulus condition, and the resultant ME, a measure of multisensory enhancement. Note that each cross-modal stimulus combination produced responses exceeding the predicted sum of the unisensory responses, a frequent consequence of combining weakly effective stimuli. **B:** a typical neuron in a dark-reared animal. It was incapable of integrating visual and nonvisual stimuli, but integrated auditory-somatosensory stimuli to produce the characteristic multisensory response. **C:** a typical neuron from a noise-reared animal. Despite failure to integrate auditory and nonauditory information, visual-somatosensory integration is intact. **$**P < 0.001.
their ability to integrate cues with which they had extensive experience.

However, significantly fewer of them were capable of visual-nonvisual integration than normal ($P \leq 0.001$ in both cases). Visual-auditory integration took place in only 17% (8/47) of them, and visual-somatosensory integration in only 11% (5/47) (Table 1). Furthermore, their respective MEs (20 and 17%) were also significantly lower than normal ($P \leq 0.001$ in both cases) and lower than their ME for auditory-somatosensory integration ($P \leq 0.001$ in both cases). The inability to integrate visual-nonvisual cues occurred despite the fact that the unsensory comparator response magnitudes used to determine multisensory integration were statistically indistinguishable from those used in auditory-somatosensory integration ($P = 0.169$) and from those used in the control cohort ($P = 0.073$). Thus the absence of visual experience selectively compromised the development of visual-nonvisual integration in trisensory neurons (see Fig. 3).

**Noise-reared group.** Functional homologies with dark-reared neurons were apparent. These neurons had larger than normal auditory receptive fields (Efrati and Gutfreund 2011), evidencing poor overlap with their nonauditory counterparts’ receptive fields. Similarly, extensive visual-somatosensory experience in the rearing environment was reflected in a normal ($P = 0.961$) proportion (75%, 38/51) of neurons that had developed the ability to integrate this cross-modal stimulus combination. They also did so at normal levels ($P = 0.207$; mean ME = 91%). However, they were far less likely than normal to integrate auditory-nonauditory stimulus combinations (see Table 1 and Fig. 2C), despite the fact that the noise-rearing paradigm provides an imperfect masking of auditory stimuli in the environment.

Only 22% (11/51) of trisensory neurons became capable of integrating a visual-auditory stimulus combination, and only 25% (13/51) became capable of integrating an auditory-somatosensory stimulus combination: much lower ($P \leq 0.001$ in both cases) incidences than in the control cohort, and lower ($P \leq 0.001$ in both cases) than their own probability of visual-somatosensory integration. Similarly, ME levels for each auditory-nonauditory combination were significantly ($P \leq 0.001$ in both cases) lower (auditory-auditory 27%, and auditory-somatosensory 26%) than in the control cohort and significantly ($P \leq 0.001$ in both cases) lower than for their own visual-somatosensory pairings. The incidence and mean ME of auditory-somatosensory integration were also lower than those for auditory-somatosensory in the dark-reared group (incidence: $P \leq 0.001$, ME: $P \leq 0.001$).

As in the case of dark-reared neurons, these differences could not be attributed to differences in the unisensory comparator responses ($P = 0.882$). Thus this rearing condition selectively compromised the development of trisensory neurons’ ability to synthesize auditory-nonauditory stimuli (see Fig. 3). Interestingly, the incidence and effectiveness of visual-auditory integration were similar in both noise-reared and normal auditory receptive fields (Efrati and Gutfreund 2011), evidencing poor overlap with their nonauditory counterparts’ receptive fields. Similarly, extensive visual-somatosensory experience in the rearing environment was reflected in a normal ($P = 0.961$) proportion (75%, 38/51) of neurons that had developed the ability to integrate this cross-modal stimulus combination. They also did so at normal levels ($P = 0.207$; mean ME = 91%). However, they were far less likely than normal to integrate auditory-nonauditory stimulus combinations (see Table 1 and Fig. 2C), despite the fact that the noise-rearing paradigm provides an imperfect masking of auditory stimuli in the environment.

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dark-reared populations (incidence: \( P = 0.754; \) ME: \( P = 0.344 \)), presumably because each rearing condition compromised one of the modalities involved in that same cross-modal pair.

**Bisensory Neurons**

The population of bisensory neurons showed developmental profiles that paralleled those of trisensory neurons (Table 2 and Fig. 4). Dark-rearing yielded a significantly lower (\( P \leq 0.001 \) in both cases) incidence of visual-nonvisual neurons capable of multisensory integration (visual-auditory: 10% , 7/73; visual-somatosensory: 14% , 4/28). However, it had no significant impact on the incidence (72%, 18/25, \( P = 0.31 \)) or the effectiveness (81%, \( P = 0.722 \)) of multisensory integration in auditory-somatosensory neurons. Similarly, noise-rearing yielded a significantly lower (\( P \leq 0.001 \) in both cases) incidence of auditory-nonauditory neurons capable of multisensory integration (auditory-visual: 19% , 14/74; auditory-somatosensory: 22% , 5/23). However, it had little impact on the incidence (74%, 29/39, \( P = 0.91 \)) or effectiveness (91%, \( P = 0.18 \)) of visual-somatosensory integration. As in the trisensory neurons, there were no significant differences (\( P > 0.05 \) in each case) in the vigor of comparator unisensory responses among these different cross-modal combinations.

**DISCUSSION**

The present results reveal that the SC multisensory circuit learns to integrate each combination of the senses individually and reflects this in the behavior of its individual neurons. Thus, although some intuitions and observations may have led to predictions to the contrary because, for example, of the significance of vision for the functional development of other senses (King et al. 1996; Putzar et al. 2007; Wallace et al. 2004; Xu et al. 2012), a neuron does not develop a general operation through which it is then able to synthesize all combinations of senses to which it is responsive. The independence with which different cross-modal associations are learned reveals a previously unappreciated complexity in the multisensory SC circuit, one that affords it the capacity to deal very differently with different cross-modal stimulus combinations, even in the same neurons. The biological basis of this is not yet understood, but its key feature is a computational segregation of sensory inputs by their pairwise affiliation. This segregation may be accomplished in a variety of ways at the circuit (Cuppini et al. 2012; Fetsch et al. 2013) or single-neuron level (Haussler and Mel 2003), or some combination of factors involving both levels. How this developmental event occurs, whether via Hebbian, homeostatic, spike timing plasticity, or some other mechanism requires further research.

These observations, coupled with prior studies (Xu et al. 2012; Yu et al. 2010), suggest that the development of these combinatorial operations is based on cross-modal signal concordance in space and time, not the specific features of the modality-specific stimuli being combined (Xu et al. 2012). Furthermore, they can develop even if their associated unisensory response properties are immature. Mature unisensory information processing does not automatically confer the capacity to integrate across modalities, and mature multisensory processing does not require unisensory maturity. Thus unisensory and multisensory development are not inextricably linked. Indeed, sensory deprivation will significantly impact unisensory development in both the visual and auditory modalities (Chang and Merzenich 2003; Efrati and Gutfreund 2011; Rauschecker and Korte 1993; Wiesel and Hubel 1965). However, as shown here, it will not compromise the development of all multisensory integration capabilities, only those involving the restricted modality. Restricting visual experience had no
WHAT DOES A NEURON LEARN FROM MULTISENSORY EXPERIENCE? 889

greater effect in this regard than did restricting auditory experience, despite the fact that the nature of this restriction was quite different. In the former case, visual input was eliminated, whereas in the latter case auditory experience was common due to the constant noise, but most transient auditory events were masked. The equivalence of the rearing conditions in this regard is, perhaps, surprising given the common view of the SC as a visually “dominant” structure.

Furthermore, their equal effectiveness in both dark-reared and noise-reared animals is interesting, given that the cross-modal stimuli that they were exposed to during early life did not produce a greater than normal incidence or magnitude of multisensory integration. This suggests that, beyond a certain point, more experience does not have an impact on this process. Thus multisensory integration appears to be optimized by factors other than total experience; most likely, it is calibrated by the informational benefits conferred by the joint consideration of two conditionally independent sensory channels (Patton and Anastasio 2003). Thus, while theoretically the system could generate more and/or larger multisensory responses, it does not do so, presumably because such responses would confer increases in salience not warranted by the information gained.

In summary, it appears that to develop the ability to integrate signals from different senses, neurons (circuits) must have experience with them in combination. Whether this merely reflects that some degree of observed covariance is necessary to form the requisite cross-modal associations, or reflects the direct encoding of the probabilities of association, is currently unknown. However, by being specific to cross-modal pairings, the developmental algorithm selectively enhances signals that are most likely to be linked to a common event. It thereby configures the system to be of particular benefit in complex environments in which the selection of targets for overt behavior is complicated by the many signals from each modality (Pluta et al. 2011).

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS


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