Dispatch

Sensory Development: Integration Before Calibration

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New findings show that corrections for sensory misalignment do not become adult-like until late childhood, whilst sensory integration develops years earlier. This calls for refinement of the theory which posits that to integrate the senses, the developing system must first be calibrated.

The brain's ability to minimise sensory ambiguity and uncertainty by combining incoming signals into a unified percept puts even the most intelligent machines to shame. The mechanisms supporting this capacity, however, remain a puzzle. In the last decade, many studies have shown that adult-like efficiency in sensory integration is challenging to acquire: adult-like benefits from integration, such as reduced perceptual uncertainty, emerge only around 8–10 years of age [1,2]. The dominant explanation for this surprisingly late development is that children's senses are still calibrating and therefore biased, rendering integration maladaptive [2,3]. For example, because retinal object size varies with viewing distance, visual size estimation is bias-prone. According to the calibration hypothesis, perceptual bias may be reduced in development by calibrating vision to view-invariant haptic size estimates, rather than integrating these cues. In this issue of *Current Biology*, Rohlf *et al.* [4] have flipped this idea on its head, suggesting instead that to cross-calibrate, the senses must first be integrated. They support this proposal with intriguing new evidence that the ability to calibrate misaligned sensory estimates develops surprisingly late, while children may combine these same discrepant cues years earlier than previously thought.

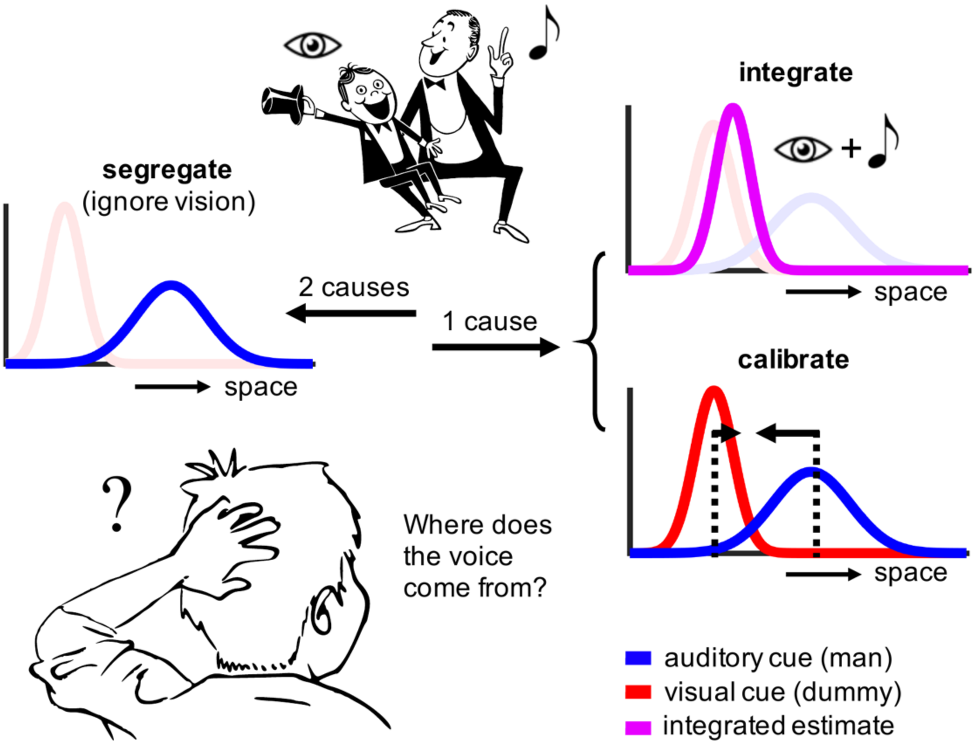

Figure 1. The ventriloquist problem. A sound is presented (the man speaks / a tone is played) while a visual distractor (the dummy's mouth movement / a flash) is shown at a spatial offset. The ventriloquist illusion occurs if the perceived sound location gets shifted towards the visual cue's position. If it appears that the dummy is speaking, you have may have inferred that both cues (visual and auditory) originate from the same cause with some probability, so they should be integrated (i.e., averaged) to improve spatial precision. In this scenario you may also conclude that your auditory and visual space maps are misaligned because they display a systematic discrepancy, and must be calibrated. In this model, the strength of the illusion depends on the prior expectation that audio-visual signals have a common cause, the reliability of the single cues (indicated by the width of their probability distributions), and their spatial discrepancy. Rohlf *et al.* [4] provide novel evidence that integration of audio-visual cues in this scenario may develop by the age of 5 years, but sensory calibration and causal inference may develop years later, by the ages of 9–10. This suggests that young children may experience ventriloquist illusions, but potentially less strongly than their parents. Ventriloquist illustration from RTRO/Shutterstock.

Sensory calibration develops late

The new data reported by Rohlf *et al.* [4] demonstrate that audio-visual calibration in a ventriloquist task [5] (Figure 1) develops late and in stages during childhood. In their study, adults and 5 to 11-year-olds located sounds along a speaker-ring by naming the animal picture perceived closest to the source. In multisensory calibrator trials, a visual distractor cue was shown at a 13.5° offset from the sound-producing speaker. These calibrator trials were interspersed with auditory-only test trials. In adults and 6 to 10-year-olds, the audio-visual mismatch shifted the perceived origin of subsequent isolated test-trial sounds in the direction of previously seen visual cues, suggesting auditory space was calibrated against vision. Surprisingly, however, this effect was absent in 5-year-olds. Why? Because even infants recalibrate their reaches to shifted visual inputs when wearing space-distorting prism glasses [6,7], it seems unlikely that 5-year-olds cannot resolve sensory conflict at all. Instead, 5-years-olds may still be learning to recognise the visual cue as a trustworthy calibration benchmark [8], to assign the two cues to a single cause, or to decide which portion of the sensory discrepancy reflects noise versus bias without explicit feedback [9].

Whilst 6 to 7-year-olds recalibrated conflicting auditory cues towards the visual cue location, a clever experimental manipulation revealed that they lacked adult-like flexibility; the auditory location cues varied in pitch, with visual distractors offset to different sides (left or right) for low versus high pitches. Accordingly, adults and 9 to 10-year-olds experienced tones presented alone as systematically shifted towards different sides depending on their pitch. Instead, 6 to 7-year-olds ignored tone-context entirely; they perceived sounds in isolation as shifted towards the last-seen visual cue, but no pitch-dependent space remapping emerged. So the ability to link specific audio-visual calibration regimes to different tone-contexts, and flexibly switch between regimes across these contexts, only developed around the ages of 9–10 years.

Together, these findings suggest that perceptual inference in new sensory environments that offer little opportunity for supervised learning may pose a particular challenge for younger children. Understanding how this affects perceptual performance more broadly, will undoubtedly be of great relevance to child educators, traffic safety experts, and developmental experimentalists.

Sensory integration develops early

Intriguingly, at all tested ages, Rohlf *et al.* [4] observed a ventriloquist effect during the multisensory calibrator trials, with perceived sound locations being pulled towards the visual distractor. The response patterns suggested that this involved sensory integration, because sounds were consistently perceived in-between the auditory and visual cue and did not follow the bi-modal distributions that might arise from switching between these cues. This evidence for audio-visual integration by 5 years of age, stands in stark contrast with reports that sensory integration only develops years later [10]. What may explain these conflicting conclusions?

One key difference between the Rohlf *et al.* [4] study and earlier work, is that the large audio-visual discrepancies in ventriloquist tasks induce uncertainty about whether the cues have a single cause (so you should integrate by computing a reliability-weighted average [11]), or two causes (so you should segregate, ignoring the irrelevant visual cue). The ideal observer model for this task [12] incorporates a causal inference process that optimally arbitrates between these two scenarios, creating an intermediate percept. Rohlf *et al.* [4] found that children and adult's perceptual judgments were both better explained by this integration model with causal uncertainty than by models that always integrate or segregate.

Most developmental research to date has involved sensory integration problems in which two cues come from a single cause and participants are instructed to use both. In those cases, adult performance most resembles an integration model and child performance a segregation model, but whether causal uncertainty offers a better developmental account is typically not tested. Interestingly, Rohlf *et al.* [4] found that the best-fitting causal inference model parameters varied with age, with younger children displaying lower prior expectations of common cause. This suggests that what develops in childhood, is not the neural infrastructure needed to integrate cues, but the criterion for *when* cues should be integrated.

These findings suggest that young children may perceive scenarios with multiple sensory cues differently from adults because they are unsure about the underlying causal structure. This uncertainty may partly stem from greater sensory bias, or higher uncertainty about sensory reliability, as suggested by a recent study [10] showing that children learnt to integrate sensory cues at younger ages after feedback training with single cues, but less so after training with both cues present. The question thus remains of whether child sensory integration is limited by sensory bias, poor estimates of sensory reliability, or lower expectation of common cause. Because Rohlf *et al.* [4] tested only a single audio-visual cue discrepancy, and used group average unisensory reliabilities from independent children for integration model-fitting, their study was not designed to distinguish these possibilities. Within-subject measures of performance across a range of cue conflicts and reliabilities, will help further untangle how causal inference, calibration, and integration interact across development. However, with the often sparse, response-bias prone data from young children [13,14], discriminating reliably between subtly different predictions from competing models is often challenging [15].

Therefore, in another route to understanding the developmental mechanisms of sensory integration, we used model-based fMRI to test for fused representations of depth cues in the brain whilst children performed a fixation task — thus circumventing performance-related confounds [16]. Evidence for sensory fusion in visual cortex emerged around the same age when children started integrating these cues perceptually in a separate depth discrimination task. This suggests that the mechanisms generating these fused representations were still developing, rather than the read-out of this information by higher-order processes. Intriguingly, if the 5-year-old brain is capable of adult-like causal inference computations, as Rohlf *et al.*'s [4] best-fitting model suggests, an integrated audio-visual space representation (linked to parietal cortex in adults [17]) should be measurable in the brain by this age.

Linking calibration and integration

What do these new findings tell us about the relationship between sensory calibration and integration? Must calibration precede integration, or *vice versa*? The answer may depend on our definitions of these processes. Rohlf *et al.* [4] make the compelling argument that integrated sensory estimates may be used to compute sensory discrepancies for cross-calibration. It would be helpful to clarify the requirements of this comparison process — is the integrated estimate crucial, or can comparisons occur at other processing stages? Similarly, the calibration hypothesis' key assumption, is that sensory integration prevents calibration, so is maladaptive for a biased system [3]. However, the predicted relationship between sensory bias reduction and the development of adult-like integration is not yet confirmed empirically, and Rohlf *et al.*'s [4] novel finding that sensory cross-calibration is slow to develop, suggests the story is complex.

Sensory calibration, segregation, and integration each require causal inference and estimation of sensory bias and uncertainty. If two sensory signals likely stem from separate causes, you should not integrate nor calibrate your estimates, even with good cross-estimate agreement. If two sensory signals likely come from one event, you must decide which fraction of the discrepancy between estimates stems from noise versus bias, to decide how to integrate (depending on cue reliability) and calibrate (depending on cue accuracy). Rohlf *et al.*'s [4] surprising findings highlight that the nature of these relationships is yet to be captured in a unified developmental model. Providing such a principled explanation, will be crucial for understanding how the well-integrated human senses are formed.

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