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Motion Perception: Slow Development of Center-Surround Suppression

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New evidence on the development of center-surround suppression in human infants shows that this key feature of visual motion perception does not emerge until seven months of age. This raises questions about the development of basic visual functions thought to derive from surround suppression.

Starting with the very first days of our lives, human neonates react to moving objects [1], something well known to parents who often entertain their babies by jingling keys or by hanging a mobile over the baby's crib. This early preference for visual motion is likely adaptive, given the critical role motion plays in our survival [2]. Infants are bombarded with sensory motion information and to successfully interact with their environment they have to learn to make sense of it. While visual experience is required for the emergence of motion processing [3], some aspects of this motion perception development are remarkably rapid. Newborns can perceive complex biological motion patterns [4], and by around seven weeks of age [5] they exhibit adult-like brain responses to moving stimuli. Yet, as reported in this issue of *Current Biology*, a seemingly basic motion-processing mechanism can take substantially longer to develop adult characteristics. Nakashima *et al.* [6] investigated the development of center-surround suppression — a fundamental and ubiquitous property of visual processing — and found that it takes seven to eight months before perceptual correlates of center-surround suppression can be observed.

In visual motion processing, antagonistic center-surround neurons respond strongly when their receptive field centers are stimulated with motion that matches neurons' preferred motion direction, but when the moving stimulus is large enough to also stimulate the receptive field surround, the neuron's response is suppressed [7]. Numerous studies have implicated this simple neural mechanism in a wide range of important visual functions, including segmentation of moving objects from their background, perceiving the shape of moving objects, aiding visual navigation and eliminating redundancies in visual signals [8]. To study human development of center-surround suppression, Nakashima *et al.* [6] relied on its putative behavioral manifestation: in motion perception, as the stimulus size increases, observers exhibit progressively increasing difficulty in perceiving motion [9]. This counterintuitive behavioral phenomenon, termed *spatial suppression*, is believed to reflect suppressive center-surround mechanisms within cortical medial temporal (MT) area [10–13]. Until now, little has been known about the early developmental trajectory of spatial suppression, and by extension, other visual abilities that might rely on spatial suppression mechanisms.

To address this gap in knowledge, Nakashima *et al.* [6] set out to measure spatial suppression strength in infants between three and eight months of age. To estimate infants' ability to perceive motion direction, they relied on a widely used novelty preference approach in which, after becoming familiarized with a stimulus, infants tend to orient toward novel stimuli. This approach works because infants can exhibit a novelty preference only if they can *perceive* a difference between the familiarized and the novel stimulus. In the familiarization phase, the drifting grating stimuli were presented on a computer screen, moving either leftward or rightwards. This phase ended when infants looked away from the monitor for at least three seconds, which was taken to indicate familiarization. During the test phase, leftward and rightward motion gratings were presented side-by-side. The idea is that infants will prefer the stimulus that moved in the different direction over the familiarized stimulus, but only if they are able to perceive the difference in motion direction between the familiarized and one of the test stimuli. Critically, to test for the presence of spatial suppression, the authors manipulated stimulus size, showing both small (4°) and large (8°) moving stimuli to infants. Here, worse performance with large stimuli is taken to indicate spatial suppression [9].

Interestingly, age made a big difference to which stimulus the infants perceived better: three to four-month-olds were more sensitive to large moving stimuli, while seven to eight-month-olds were more sensitive to smaller moving stimuli. In other words, adult-like spatial suppression was only observed in older infants (Figure 1A, left). These results nicely parallel the relatively late development of neural center-surround suppression in kittens [14]. Next, Nakashima *et al.* [6] ruled out an important confound associated with poor visual contrast sensitivity in young infants. This matters because spatial suppression weakens and eventually disappears at low contrasts [9]. But even when the stimulus contrast for older infants was reduced to match the contrast sensitivity of younger infants, the results still persisted in seven to eight-month-olds. Evidently, the absence of spatial suppression in the younger infants was not due to their poor contrast sensitivity. Together with other experiments in the paper [6], these results show that, during the first year of our lives, our motion perception progressively becomes more spatially focal, gradually exhibiting

suppressive properties that indicate development of center-surround suppression. Given a range of important visual functions that have been associated with center-surround suppression [8], this marks an important milestone in our perceptual development.

With the new results of Nakashima *et al.* [6], we now know that spatial suppression, akin to many other perceptual and cognitive processes [15], exhibits an inverted U-shaped trajectory from childhood to old age. Mirroring results for younger infants, older adults tend to excel at perceiving large, high-contrast moving stimuli. In fact, older adults can often perceive such stimuli better than their younger counterparts [16]. In addition, preliminary results show that while spatial suppression is present in five-year-olds, it is weaker than suppression observed in young adults [17]. Putting these results together, we see that the development of spatial suppression during childhood is mirrored by a gradual decline in spatial suppression in senescence (Figure 1).

Given these age-related changes in spatial suppression, an obvious question arises: How does this affect our visual behavior? A recent study [18] found that better perception of large moving stimuli (weaker spatial suppression) comes at an important cost: older adults (and younger adults with weak spatial suppression) exhibited difficulties seeing moving objects on moving backgrounds [18]. Notably, training improved the ability of older adults to see such moving objects, and it did so by strengthening spatial suppression. Thus, by suppressing background motion signals, spatial suppression appears to play an important functional role of helping us better see moving objects in dynamic visual environments [18]. Given the results from Nakashima and colleagues, we can hypothesize that young infants will have difficulty picking up moving objects when the background is also moving.

In addition to understanding its functional role, another key question pertains to the neural mechanisms that give rise to spatial suppression and account for observed age-related changes. This remains an open research question. In addition to age, individual differences in spatial suppression have been associated with higher cognitive

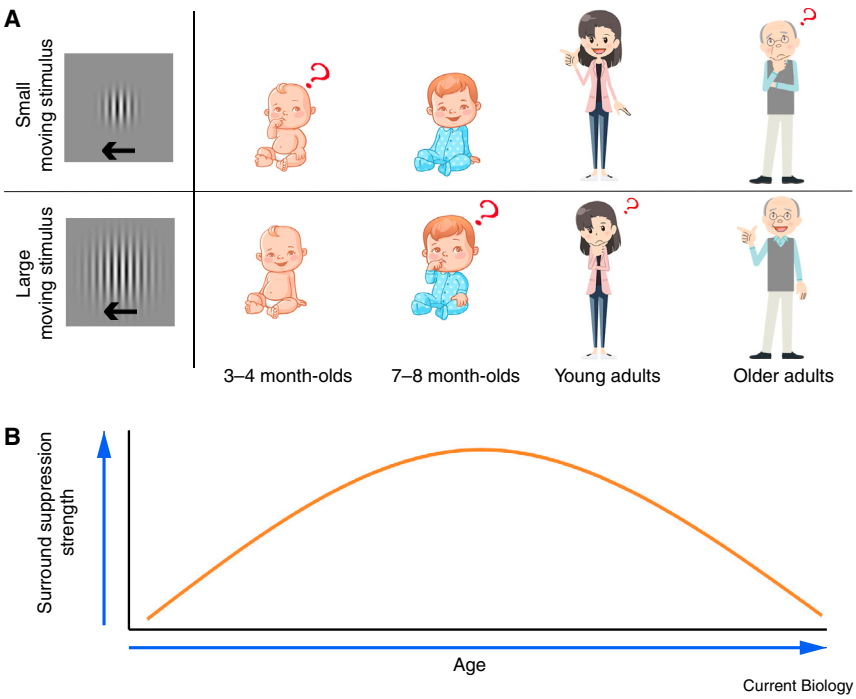

Figure 1. Developmental trajectory of spatial suppression.
(A) A cartoon illustrating how motion perception of large and small moving stimuli varies across human lifespan. Spatial suppression is evident as poor perception of large moving stimuli [9], as exhibited by seven to eight-month-olds [6] and young adults [9]. Spatial suppression is absent both for younger infants [6] and for older adults [16], resulting in an inverted U-shaped lifespan trajectory (B).

functions such as IQ [19] and a number of significant disorders, including schizophrenia and depression [8]. This suggests that spatial suppression might reflect a range of underlying neural mechanisms. Early work linked variations in spatial suppression with the GABAergic system [16]. By definition, spatial suppression involves suppression (inhibition) of visual signals from large moving stimuli. Moreover, groups that exhibit weaker suppression have been linked with impairments in the GABAergic system [8]. So, one reasonable speculation is that both the absence of spatial suppression in young infants and its deterioration in older adults derives from the reduced efficacy of GABA-mediated inhibitory mechanisms, which appear to have a similar developmental trajectory [20]. However, recent work has questioned this simple and appealing explanation. Pharmacological manipulation of GABA in primate area MT was found not to alter center-surround suppression, only affecting the overall neural firing rate [11]. And in humans, administration of lorazepam, a drug that increases GABAergic efficacy, was surprisingly found to decrease spatial suppression strength [12]; this study also found no relationship between individual differences in GABA concentration and variations in spatial suppression.

If spatial suppression is not primarily related to GABA, then what could it be? Recent work [13] showed that, while perceptual insensitivity to large moving stimuli can be linked to neural surround suppression, it also depends on noise correlations among neurons and how neural responses to moving stimuli are read-out. Both of these factors are fundamental features of sensory neural coding. Thus, assuming that these links are further substantiated, spatial suppression could become a useful tool to study the perceptual consequences of neural noise correlations. For example, one hypothesis is that the absence of spatial suppression in infants and older adults may be related to age-related changes in neural noise.

The new study by Nakashima *et al.* [6] is an important first step in examining the development of center-surround suppression in humans. Surprising absence of spatial suppression in

younger infants mirrors results reported for older adults [16]. Looking forward, this work opens the door to developmental study of visual functions that have been associated with center-surround suppression.

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Neuroscience: A New Golden Age for Neurourology

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The pons contains neurons that control urinary bladder function. Using the modern tools of neurobiology, new studies reveal a heterogeneous population of neurons which interact with higher centers and the sacral and lumbar spinal cord to coordinate complex voiding behaviors.

Almost a century ago Frederick Barrington at University College London in a now classic paper first suggested that a cluster of neurons within the pons exerted regulatory control over the lower urinary tract [1]. Today this collection of neurons is known as Barrington's nucleus. The paper consisted of a collection of observations about the types of ensuing voiding dysfunction (urinary frequency or retention) that resulted after a series of lesioning experiments in the pons of cats. This study was done with borrowed stereotactic equipment, and the paper contained no formal methods section, but his basic premise has stood the test of time [2]. Today it is widely accepted that the pons contains a neural circuit that regulates lower urinary tract function, but how does it accomplish this? In a study reported in a recent issue of *Current Biology*, Verstegen *et al.* [3]. have skillfully used the latest tools of modern neurobiology to answer some very basic questions about the functional role of Barrington's nucleus; their findings contribute to a better understanding of the mechanism(s) of central neural control over lower urinary tract function.

For 90 years, the basic methodology for studying this complex circuit (Figure 1) used selective lesioning [4] as well as electrophysiology studies combined with