## Motion Perception Getting Better with Age?

Older people can discriminate visual motion of large, high-contrast stimuli better than young adults. This surprising result, reported by Betts et al. in this issue of *Neuron*, suggests weaker center-surround antagonism in senescence, perhaps attributable to agerelated reduction in GABA-mediated inhibition.

As any older adult (including the second author) will tell you, getting old has its annoying consequences. Everyone worries about decreased mobility and losses in cognitive function (including memory). Less appreciated but equally troublesome is the toll aging takes on the senses: taste and smell are dulled, and hearing gets tougher, especially in noisy environments. Alas, vision is not spared by years of wear and tear-even in the absence of disease or injury, we all can expect to suffer age-related losses in near vision, dim light vision, depth perception, and object recognition (Spear, 1993; Sekuler and Sekuler, 2000). Given this sobering prognosis, older individuals will be intrigued to read the seemingly good news contained in a recent study by Betts and colleagues, published in this issue of Neuron (Betts et al., 2005). Their work has revealed an aspect of vision, in particular visual motion perception, wherein older individuals actually outperform younger folks. Alas, this "superiority" in motion perception may come about from neural changes whose ramifications are not so exciting. Still, the discovery is highly newsworthy, and in a nutshell here's the story starting with the background.

One of the many neurophysiological changes associated with aging is reduced efficacy of cortical inhibition, specifically GABA-mediated inhibition (Leventhal et al., 2003). This loss is noteworthy because cortical inhibition plays a critical role in all sorts of brain functions, including decision-making within winner-take-all networks, sharpening of tuning curves of sensory neurons, and maintaining the brain's metabolic demands within reason. Thus, age-related reduction in GABA could have detrimental consequences on a broad range of cognitive, perceptual, and behavioral functions. For instance, broader tuning curves in visually activated neurons could adversely affect discrimination thresholds (Leventhal et al., 2003). Furthermore, weakened inhibitory processes may fail to keep irrelevant information from working memory, thus reducing its functional capacity in senescence (Hasher and Zacks, 1988).

Within vision, two key, interrelated functions of inhibition are the *attenuation* of neural signals associated with uninformative or redundant regions in the image and the *accentuation* of regions in the image where there exist discontinuities in luminance, color, depth, or motion. As a rule, "uninformative" regions of the visual field correspond to relatively large expanses of the image containing little or no variation in appearance. These uniform regions contain minimal information, and not surprisingly, they evoke very little neural activity in visual cortex. Inhibition is an effective means for dealing with visual monotony.

In vision, suppression of activity is generally accomplished by antagonistic center-surround circuitry-a simple yet ubiquitous and computationally powerful neural mechanism. An antagonistic center-surround neuron will respond strongly when its receptive field center is stimulated with that neuron's preferred stimulus (e.g., a grating comprising rightward moving contours). When the size of the stimulus is enlarged so that it fills both the center and surround regions of the neuron's receptive field, that neuron becomes suppressed-i.e., center-surround neurons will respond poorly to large uniform stimulation. Inaugurated in the retina, center-surround antagonism is found at multiple stages of visual processing (Allman et al., 1985), suggesting that significant changes in the relative strength of surround suppression should have a measurable effect on visual perception.

Now, how would decreased efficacy of cortical inhibition, as one of the consequences of aging, affect processing carried out by inhibitory center-surround mechanisms? This is the question investigated by Betts and colleagues. A consequence of reduced surround inhibition would be increased neural responsiveness to large uniform stimuli. This suggests the possibility that reduced cortical inhibition could increase an observer's sensitivity to visual input that is normally suppressed. In such a case, we would have a situation where an abnormal physiological change (i.e., reduced inhibition) would lead to improved visual sensitivity, albeit to a relatively uninteresting visual stimulus.

In their exploration of potential effects of age-reduced inhibition on vision, Betts et al. focused on motion perception. This was a fitting choice, because the neurophysiology of center-surround antagonism in motion processing has been well documented (Tadin and Lappin, 2005). Furthermore, center-surround motion mechanisms are believed to have measurable behavioral consequences: as the size of a high-contrast moving stimulus increases, a typical observer shows a dramatic increase in direction discrimination thresholdsit becomes harder to judge in which direction a set of contours is moving. This deterioration in performance likely reflects a reduction in responsiveness of centersurround motion neurons as the size of the moving stimulus expands beyond the receptive field center (Tadin et al., 2003). On the other hand, when the stimulus is low contrast, increasing stimulus size actually improves direction discrimination, as one would expect based on spatial summation. This contrast-dependent switch from suppression to summation has been documented neurophysiologically in motion-selective neurons in middle temporal area (Pack et al., 2005). So what happens when these psychophysical measures of



Figure 1. A Younger and an Older Observer Performing a Direction Discrimination Task

The stimulus is a large, high-contrast moving grating.

motion discrimination are analyzed in older people, whose GABA-mediated inhibition is putatively weaker?

The task used by Betts and colleagues was simple: a moving grating briefly appeared on a computer screen, and an observer indicated the perceived direction by a key press (left versus right). In different conditions, gratings were varied in size and in contrast. For young observers, the findings matched our published results (Tadin et al., 2003): at high contrast, performance deteriorated with increasing size, indicating spatial suppression, but at low contrast, performance improved with size, indicating spatial summation. In other words, the motion of large, high-contrast gratings was, paradoxically, more difficult to discern than the motion of large, low-contrast gratings.

The elderly observers in the Betts et al. study, however, exhibited a different pattern of results. At low contrast, their thresholds decreased (i.e., performance was better) with increasing grating size, the same summation effect seen in younger people. It is true that, on average, thresholds for the older participants were somewhat elevated, which is hardly surprising given what we know about vision and aging. The surprising outcome occurred when older people were tested using high-contrast moving gratings. Here, motion discrimination thresholds varied hardly at all with grating size, providing no hint for the involvement of surround suppression. Thus, because younger observers' thresholds increase dramatically with increasing size while older observers' thresholds remain stable, older observers are able to perform motion judgments under conditions where younger observers find the task impossible (Figure 1). That's the surprising, "good news" aspect of the Betts et al. study.

But is this really good news for the elderly? To answer this question, let's consider why their performance is better. Betts and colleagues provided a relatively straightforward explanation: if one assumes that poor ability of young observers to perceive large, highcontrast moving objects is a perceptual correlate of strong center-surround antagonism (Tadin et al., 2003), then the lack of a similar size-dependent decrease in performance for elderly observers may indicate decreased potency of surround inhibition. This conclusion squares, of course, with the decreased efficacy of



Figure 2. A Younger and an Older Observer Performing a Shape Discrimination Task

The stimulus is a rectangular shape moving in a different direction than the background.

GABA-mediated inhibition in older brains (Leventhal et al., 2003).

Unfortunately, this conclusion, if substantiated, carries with it some negative ramifications. If one thinks of large moving fields as moving *backgrounds* and smaller moving stimuli as moving *figures*, then weak surround suppression would suggest weaker sensitivity to moving figures and, more importantly, an inability to "ignore" background motion. It is important to note that this line of reasoning also applies to *physically* stationary backgrounds, because eye and head movements frequently cause such backgrounds to move on our retinae. Thus, it may become more difficult to segregate moving objects from their backgrounds without the assistance of surround suppression (Figure 2). Indeed, older observers have great difficulty perceiving the shape of objects defined by motion (Wist et al., 2000).

Future research should more closely examine functional consequences of the observations reported by Betts and colleagues. Such work not only will shed light on presently speculative links between abnormal center-surround suppression and visual dysfunction in senescence, but also will help us understand functional roles of center-surround inhibition in normal vision. Furthermore, we still know very little about the extent to which visual mechanisms other than center-surround antagonism are affected by age-related weakening of inhibition. For example, age-related decline in the ability to discriminate small differences in motion direction (Ball and Sekuler, 1986) may derive from diminished cortical inhibition and associated broadening of neuronal selectivity. Clearly, a large number of outstanding questions remain. Their resolution will require converging evidence from psychophysical studies and primate research where GABA levels can be experimentally manipulated (Leventhal et al., 2003). We can all hope that this line of research will eventually yield treatment options for some of the problems that await us in old age.

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