
Visual Perception and Aging

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Abstract A series of studies performed in our laboratory on aging and its effect on perceptual processing and working memory capacity for visual stimuli are reviewed. Specifically, studies on luminance, colour, motion, texture, and symmetry processing are reported. Furthermore, experiments on the capacity to retain size and spatial frequency information are also discussed. The general conclusion is that there are a number of perceptual abilities that diminish with age. However, the extent of these deficits will depend on the complexity of the neural circuitry involved for processing a given task. This is also true for visual working memory where no evidence of loss due to aging is demonstrated for processing low-level visual information, when individual differences in sensory input are compensated for. It is concluded that perceptual processing deficits due to aging (like working memory) will become evident when the computational load reaches a certain level of complexity (larger or more complex network) even if the tasks remain cognitively simple.

Throughout life humans interact with the environment in response to their perception of the world. In the early stages of development, the world as we perceive it changes rapidly. We are born with rudimentary pre-set abilities that are refined in early life by maturation and interaction with the environment. The capacity to perceive the world correctly reaches a high level of sophistication that is unparalleled by any artificial system. Regardless of the very complex processing required to adequately represent the external world, our abilities become so refined and automatic that we are unaware of the immense computation required to perceive it. During adulthood, our sensory and perceptual abilities also change but these changes are usually subtle, often gradual, so they are seldom noticed. However, under controlled laboratory conditions, it is possible to isolate perceptual functions that are clearly

affected by aging.

Until recently, there has been little emphasis in the scientific literature on the consequences of aging on visual perception, although there has been a substantial amount of work on higher cognitive abilities. The work on visual perception has been somewhat contradictory because some perceptual abilities appear relatively spared while others are affected by aging. In the present paper, I will report studies performed in our laboratory that attempt to determine what perceptual abilities are or are not affected by aging, and why performance of the elderly may differ in different contexts.

Anatomical and Physiological Effects of Aging

Although individuals over 65 years of age currently make up more than 10% of the population and represent the fastest growing segment of the population (U.S. Administration on Aging, 1991), our understanding of the nature and cause of visual changes in the elderly remains limited. The risk of visual impairment is elevated in elderly individuals: Each of the four leading causes of blindness in North America has a higher incidence in the elderly (macular degeneration, glaucoma, diabetic retinopathy, and cataracts). Some elderly individuals suffer profound visual loss and blindness, but many others exhibit less severe visual dysfunction, which nevertheless impairs their ability to function efficiently (Kosnik, Winslow, Kline, Rasinski, & Sekuler, 1988; Spear, 1993). The extent to which particular anatomical and physiological changes contribute to specific visual deficits in the healthy elderly remains unresolved. In addition, it is not known whether all visual capacities deteriorate at the same rate.

Virtually every structure in the primary visual pathway undergoes some degree of nonpathological age-related change (for a review, see Spear, 1993). At the photoreceptor level, rods seem to be more vulnerable than cones as rod numbers decrease and cone numbers remain stable with age (Curcio, 2001). In the retinal ganglion cell layer, density decreases with age, a

change that is especially marked outside the macular region (Harman, Abraham, Moore, & Hoskins, 2000).

Early anatomical and physiological work on age-associated cortical changes reported a loss of cells whereas more recent work points towards functional changes (Peters, Moss, & Sethares, 2001; Peters, Rosene, Moss, Kemper, Abraham, & Tigges, 1996; Spear, 1993). Changes reported in the visual cortex of monkey include a decrease in cell density and a synapse loss in layer 1 of V1 (Peters et al., 2001), and a degradation of the myelin sheath of axons but no loss of nerve fibers per se (Nielsen & Peters, 2000; Peters, Moss, & Sethares, 2000). These changes extend beyond the visual cortex and seem to correlate well with behavioural measures of age-associated cognitive decline (Peters et al., 1996).

A Bottom-Up Approach

Perceptual abilities are directly affected by sensory input. For this reason, the present paper will focus on studies that have attempted to control or explain the effects of sensory losses that occur with aging in relation to their impact on perceptual processing. Furthermore, we will focus on the basic visual attributes as it is hypothesized that the brain will process a visual image by analyzing its different attribute characteristics. Such a modularity of perceptual information has been suggested earlier by Marr (1980) and refined by Cavanagh (1988). Essentially, we can break down an image into individual components (attributes) that define the objects within it. There are five main attributes, namely, luminance, colour, motion, texture, and depth. The first two attributes (luminance and colour) have to be initially processed because all other attributes are derived from this information. For this reason, any object in an image that is defined by luminance or colour is said to have a "first order" property. If an object can only be defined by motion, texture, or depth (without any luminance or colour cues), it is said to have "second order" properties because additional processing is required to perceive the image (Cavanagh & Mather, 1989).

What is Stimulus Complexity?

An important principle inherent in the present paper revolves around the notion of stimulus complexity. As mentioned above, stimulus complexity can be defined by second- versus first-order properties of an image where second-order properties involve additional processing for the brain to make sense of an image.

A stimulus can also be defined as more complex if the correct perception of it requires the processing of more than a single first-order (or second-order) attribute. For instance, if to compare the size of two

images one would have to process both colour and luminance, as opposed to only one of these properties, we can assume that additional processing would be required to compare the information available in one attribute with information from another.

Another notion of complexity involves the spatial configuration of an image. Symmetrical images represent a particular example of how spatial configuration can elicit additional properties. If 100 dots are randomly presented in a circular area, one will perceive a circle with a textured surface. However, when both halves of the circle are composed of randomly positioned dots that are mirror images of one another about a vertical axis, then an additional property becomes apparent and the circle appears as two half circles with a clear axis in the centre even if none of the dots may contact each other. This property comes about because the visual system makes comparisons relative to the putative axis, implying additional processing.

Stimulus complexity from spatial configuration can also occur when objects to be compared are presented in different spatial locations as opposed to the same location. For instance, if one is to compare two shapes that are presented simultaneously (spatial forced choice) as opposed to when they are compared in sequence (temporal forced choice) for the same locations, then additional processing may be required when the object shapes are encoded simultaneously.

Stimulus Complexity and Processing Stages are not Necessarily Analogous

Another important distinction to make in the context of the present paper regards the concepts of processing stage and stimulus (or processing) complexity. It is well known that the visual system has a somewhat hierarchical structure where information is processed at one level and then transferred at another stage for a different analysis or function. For instance, an image is first detected (sensory processing) and the information is passed on to another level of processing (perceptual processing) for integration and further analysis. Once the information is perceived, it is then stored in working memory where it is compared with previously stored information. These processing stages are dynamic and highly interactive. It has been demonstrated that some high-level perceptual functions, such as discriminating radial frequency patterns, solicit extrastriate areas, but human observers are extremely efficient at this task where performance reaches hyperacuity levels (Wilkinson, James, Wilson, Gati, Menon, & Goodale, 2000; Wilkinson, Wilson, & Habak, 1998). It is therefore possible that some higher-level processes are more hard-wired and therefore may be less complex for the visual system to perform.

It is argued here that both the perceptual and working memory stages can have their own levels of complexity. For instance, at the perceptual stage, it is generally believed that first- and second-order stimuli have different levels of complexity even if the task is identical. By the same logic, working memory may also involve simple and complex processing. For instance, the difference between storing a simple element such as a square versus storing multiple elements would inevitably require different levels of processing.

It has been demonstrated that aging can affect processing at each stage to varying degrees. The question of when each of these processing stages is affected by aging is the main focus of our work. In the present paper, I propose a working hypothesis that visual perception and working memory will be particularly affected by aging when the stimuli presented require more elaborate (complex) processing based on the definitions presented above.

The Effect of Aging on Sensory-Perceptual Processing of Visual Information (Attributes)

Prior to the discussion on complex perceptual processing, I will briefly review work on the effect of aging on the processing of primary visual attributes, namely luminance and colour. These sections will be followed by a discussion on perceptual processing at varying levels of complexity and their relation to aging. Studies on working memory and its relation to visual perception and aging will follow and, finally, a discussion of the theoretical implications of these results will be presented.

LUMINANCE

Most of the research on aging vision has been concerned with the sensitivity for luminance or luminance-defined forms. A number of studies show that there is a visual acuity loss with age (Kline & Scialfa, 1996; Pitts, 1982; Weale, 1982). Other studies have demonstrated that spatial contrast sensitivity for static sinusoidal gratings is also diminished with age (Crassini, Brown, & Bowman, 1988; Elliot, Whitaker, & MacVeigh, 1990; Sloane, Owsley, & Alvarez, 1988). These results primarily show a loss at medium and high spatial frequencies, a loss that cannot be explained solely by optical factors. Studies of spatio-temporal interactions have also shown selective losses for the elderly where the sensitivity for medium to high spatial frequencies is reduced at low temporal frequencies, whereas the sensitivity for all spatial frequencies is affected at high temporal frequencies (Elliot et al., 1990; Sloane et al., 1988). Some researchers have demonstrated that there is a loss of flicker sensitivity with aging and that the loss may be accentuated at higher temporal frequencies

for foveal vision (Tyler, 1989), and may show preferential loss in certain areas of the visual field (Casson, Johnson, & Nelson-Quigg, 1993). We have recently assessed temporal modulation visual fields or TMFs (Faubert, 1991) with a number of observers ranging from 20 to 70 years of age (Faubert, 1998). The task of the observer was to detect one- and two-degree targets flickering at either 2 or 16 Hz temporal frequency. The stimuli were contrast modulated about the mean luminance of the adapting field to establish contrast sensitivity for each of the points assessed. Forty different points within a 40-degree visual field were evaluated (see Faubert 1991 for methodological details). The data clearly demonstrate that there is an effect of normal aging on TMFs. However, different patterns of losses emerge when the targets are flickering at 2 Hz as opposed to 16 Hz, demonstrating that age-related losses can be parameter specific even for low-level processing and are important in light of what we know about the effect of age-related ocular diseases such as glaucoma on TMFs (Faubert et al., 1987a,b, 1989). The first obvious visual consequence of glaucoma is a visual field constriction, which often appears even before anatomical signs of neural degeneration. TMFs have been shown to be a more sensitive measure of such a loss than standard perimetry testing (Faubert et al., 1987a,b, 1989) and studies demonstrate that glaucomatous loss may be more important when stimuli are flickered at higher temporal frequencies (Tyler, 1989). A certain number of older observers have normal tension glaucoma and may represent decreased sensitivity in peripheral vision without showing any other signs of disease and without knowing that they have glaucoma. These data emphasize the importance of compensating for sensory input when studying higher stages of visual processing such as visual perception and working memory.

COLOUR

At the photoreceptor level, there have been reports of age-related losses for short (S), medium (M), and long (L) wavelength cone mechanisms (Knau & Werner, 2000). However, most of the age-related losses have been attributed to the short wavelength system (Ruddock, 1965; Verriest, 1970; Werner, 1982). Little work has been done to determine the effect of aging on colour perception. Johnson and Marshall (1995) have demonstrated that there is a loss associated with colour opponent mechanisms, implying that the loss also occurs beyond the receptors. Fiorentini and colleagues have shown a mild effect of age on both chromatic and luminance systems, which appear to be affected evenly (Fiorentini, Porciatti, Morrone, & Burr, 1996).

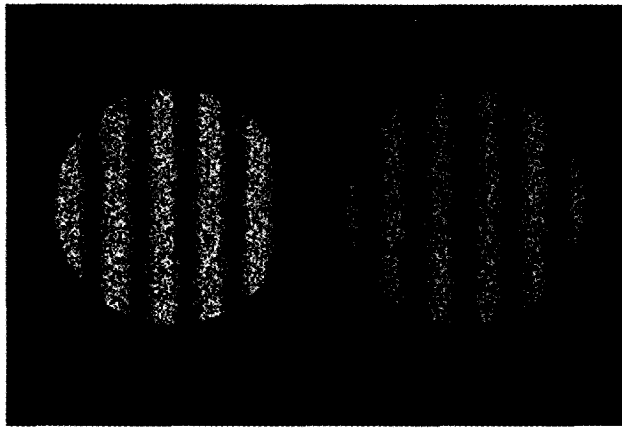


Figure 1. Examples of first-order (left) and second-order (right) stimuli used in the Habak and Faubert (2000) study.

We have recently conducted a study to determine the relative weights of optical, receptor, and postreceptor factors on the diminished colour processing in aging using the motion nulling technique (Nguyen-Tri, Overbury, & Faubert, 2000). A number of motion-nulling studies have demonstrated that colour mechanisms do contribute to the perception of motion (Bilodeau & Faubert, 1997, 1999; Cavanagh & Anstis, 1991; Faubert, Bilodeau, & Simonet, 2000; Webster & Mollon, 1997). For a more detailed discussion on the motion-nulling procedure, please refer to Faubert and colleagues (Faubert et al., 2000). When a motion stimulus contains two sinusoidal gratings moving in opposite directions, there is a perceptual competition as to which direction the combined stimulus is seen as moving. If the sine wave grating with the leftward motion has a greater perceived contrast, a leftward motion will be perceived and vice versa. When the two opposite moving gratings are perceived as equivalent, there is motion nulling in the sense that the combined stimulus is perceived as counterphase flickering, and the result is that there is no clear motion direction. We first determined isoluminance values for observers of different ages. We do this by opposing two coloured gratings that generate opposite motion directions. We maintain one of the colour inputs constant while manipulating the intensity of the other colour. When the two are perceived as having the same strength, the result is counterphase flicker. From this we can determine the intensity required by one colour (e.g., green) to oppose another (e.g., red). If lenticular senescence is the primary factor for colour vision changes, the age-related losses should be primarily accounted for by isoluminance values. We then conducted motion-nulling experiments by opposing an isoluminant red-green stimulus moving in one direction to an achromatic

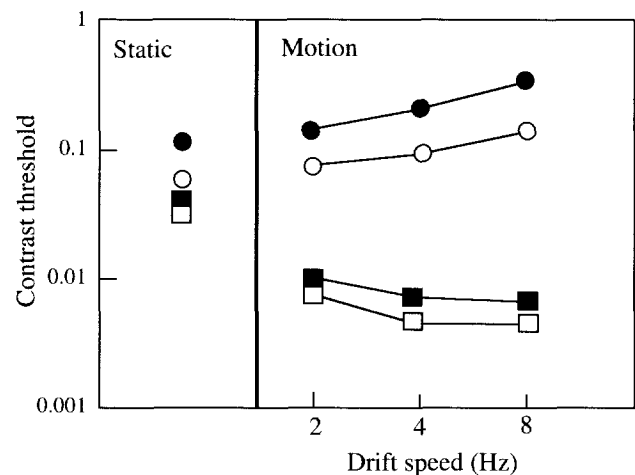


Figure 2. Contrast thresholds for young (open symbols) and older (closed symbols) observers. The first-order stimuli are represented by squares and the second-order stimuli by circles. The error bars are obscured by the symbols. Adapted from Habak and Faubert (2000).

(black-yellow) stimulus moving in the opposite direction. The amount of contrast necessary for the achromatic grating to oppose the isoluminant grating represents the relative contrast input of the chromatic system to motion. If the reduction of chromatic processing is due to postreceptor colour mechanisms, we should expect age-related deficits in this task. The overall results demonstrate that the majority of the age-related deficits can be accounted for by optical and receptor factors, and there is no clear evidence of an age-related deficit of chromatic processing when we account for the early-level factors.

The implication here is that motion perception generated by a 1st order property, such as colour, does not appear affected by normal aging if one compensates for individual differences in sensation. As discussed in the next section, this is also true for luminance-defined first-order motion and texture.

MOTION PERCEPTION

Motion sensitivity also appears to be impaired in the elderly and it has been shown for both first-order (Wood & Bullimore, 1995) and second-order motion processes (Trick & Silverman, 1991). This loss appears to be more accentuated in foveal as opposed to peripheral vision (Wojciechowski, Trick, & Steinman, 1995). In studies where vehicular motion judgments were assessed, the older observers show a diminished capacity to accurately judge velocity changes (Scialfa, Guzy, Leibowitz, Garvey, & Tyrell, 1991) and have poorer verbal estimates of arrival time demonstrating that the

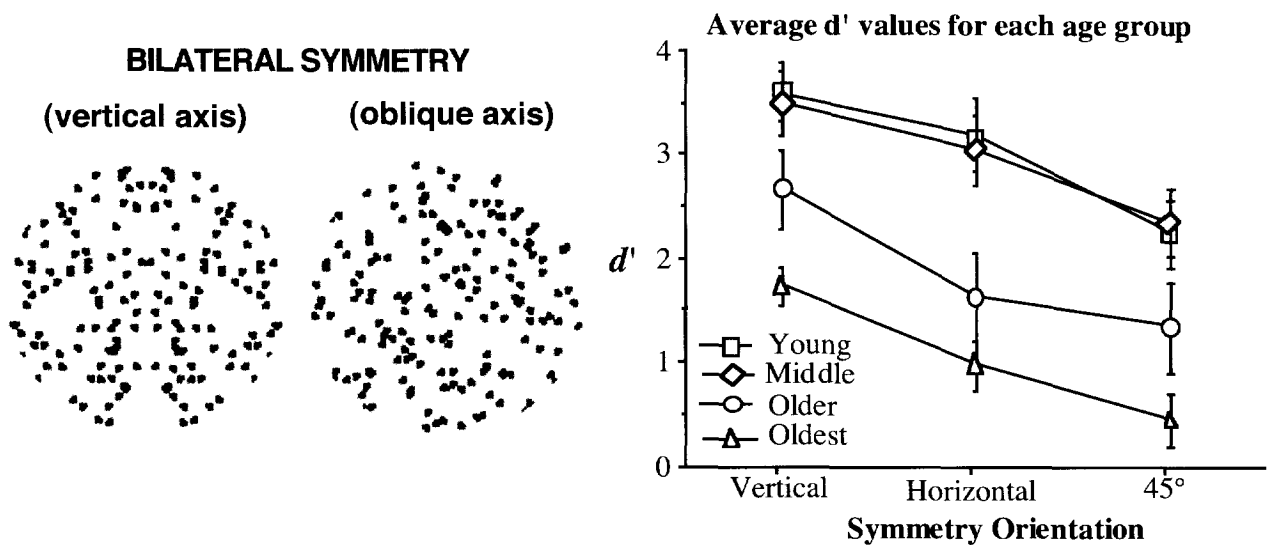


Figure 3. Examples of symmetrical patterns used in the Herbert, et al. (2002) study (left). The graph shows the d' value for the different age groups. The older groups represent observers above 60 years of age.

use of motion information may be affected (Schiff, Oldak, & Shah, 1992).

In a recent study, we have demonstrated that it may be the type of processing and not motion perception per se that is affected by aging (Habak & Faubert, 2000). The perception of stimuli that were either simple (first-order or luminance-defined) or complex (second-order or texture-defined) was compared. We demonstrated that, despite identical spatio-temporal parameters and task for these two stimulus types, aging affected the stimulus requiring the more complex cortical processing. Figure 1 demonstrates how a first- and second-order stimulus appeared in our displays. The second-order stimulus is known to require more cortical processing levels (Smith, Greenlee, Singh, Kraemer, & Hennig, 1998; Wilson, 1998). The results for the two groups are shown in Figure 2. We found similar results for the static pattern data (texture, see Figure 2, left), which demonstrates that the age-related loss is not attribute-specific (i.e., specific to motion) but *processing*-related.

SYMMETRY PERCEPTION

A particular instance of texture processing is evident under conditions of symmetrical patterns. Most structures in our environment, whether they are physical or biological, have symmetrical properties. Detecting bilateral symmetry requires the ability to integrate information across an image, because corresponding activity must be found at symmetrical locations across a putative symmetry axis.

To my knowledge, we have conducted the first

study on the effect of aging on the capacity to detect symmetrical patterns (Herbert, Overbury, Singh, & Faubert, 2002). Symmetry detection was examined for different age groups because this is a visual task that has been suggested to rely on both the integrity of low-level visual functions (e.g., Dakin & Herbert, 1998; Gurnsey, Herbert, & Kenemy, 1998) and/or higher level factors related to spatial perception (Labonté, Shapira, Cohen, & Faubert, 1995; Palmer & Hemenway, 1978; Rock, 1983; Rock & Leaman, 1963). Bilateral symmetry (where one half of a pattern is a mirror reflection of the other half) can be detected when the halves of a pattern are separated by several degrees (Jenkins, 1982; Labonté et al., 1995; Tyler & Hardage, 1996), so there are relatively long-range comparisons that can be made. Some research on symmetry detection has indicated that top-down influences occur in that attention and priming influence the salience of symmetry at different orientations (Pashler, 1990; Wenderoth, 1994; Wenderoth & Welsh, 1998).

One might expect symmetry detection to decline with age because of age-related changes in higher cortical functions. Thus, changes in the salience of symmetry with increasing age could provide an index of how long-range visual connections change during the lifespan. We found that observers over the age of 60 show a decreased capacity for distinguishing symmetrical versus nonsymmetrical patterns. The data are shown in Figure 3 and are presented as d' values. There was no age by symmetry axis orientation interaction so whatever mechanism is affected by aging, it is not selective to a given orientation.

Barlow (Barlow, 1978; Barlow & Reeves, 1979) has argued that dot stimuli like the ones used in our symmetry experiment are ideally designed for studying "mid-level" processes in vision. Specifically, he argues that the high-contrast dots are easily transduced by the peripheral visual system, and therefore that limitations on performance will be due to higher-level processes. We can therefore assume that the aging effect observed in our study is the consequence of higher processing requirements not likely caused by low-level sensory losses.

DEPTH AND BINOCULAR VISION

Several reports have also indicated an effect of normal aging on binocular processes (Faubert & Overbury, 2000; Speranza, Moralia, & Schneider, 1995) and stereodepth (Wright & Wormald, 1992; Yap, Brown, & Clarke, 1994). The prevalence of defective stereopsis showed that in a population of 728 individuals over 65 years of age, 27% had full stereopsis and 29% had no stereopsis when measured with the Frisby stereotest (Wright & Wormald, 1992). It was also determined that the stereopsis decline in the elderly did not result from reduced retinal illumination related to optical factors (Yap, Brown, & Clarke, 1994).

The fact that stereopsis (a second-order process) and binocular summation (both assumed here as involving more complex processes than monocular function) declines with age implies that increased processing demands generate age-related losses.

Visual Working Memory (VWM)

Once a stimulus is processed, the next level up involves storing this information for future comparisons. There has been a recent growing interest in working memory (WM), a brain system that provides temporary storage of information and manipulates this information to perform cognitive tasks. WM, as described by Baddeley (1986), has a sensory storage buffer in which information can be held for a short period of time and a central executive system responsible for performing computations and transformations.

Studies on WM have traditionally focused on verbal and visuospatial material. Recently, researchers have examined WM for purely visual material, thus providing a link between WM and basic visual processing by examining how a stimulus is maintained in memory when it is defined by a simple visual attribute. Studies have found that luminance-defined spatial frequency and velocity information are well preserved in VWM for periods up to 10 seconds or more (Magnussen & Greenlee, 1992; Magnussen, Greenlee, Asplund, & Dyrnes, 1990; Regan, 1985). In contrast, oriented lines, contrast information, and vernier offsets show a slight

decay for such time intervals (Fahle & Harris, 1992; Lee & Harris, 1996; Vogels & Orban, 1986). Thus, it appears that some visual attributes produce a more robust memory trace than others.

Magnussen, Greenlee, Asplund, and Dyrnes (1991) described the disruption of VWM for spatial frequency with the presentation of a memory mask during the retention interval. Higher discrimination thresholds were obtained when the spatial frequency of the mask differed from the reference grating by 1-1.5 octaves and greater. Discrimination thresholds were equal when the mask and reference grating were of similar spatial frequency. Orientation, duration, and presentation time of the mask had no additional effects on threshold. Magnussen et al. (1991) interpreted their results as strong suggestion that VWM shared the same representation as sensory information. Bennett and Cortese (1996) confirmed the finding of Magnussen et al. (1991) and further reported that the effect of the mask was based on distal and not proximal frequency.

It is generally agreed that older individuals experience difficulties with WM (see Craik & Jennings, 1992, for review). Factors that have been proposed to account for a reduction of WM in aging include a reduction of processing resources, slower processing abilities, and increased difficulty to inhibit irrelevant information (Zacks & Hasher, 1997). To date, studies on aging and VWM for simple visual attributes report no loss of information for vernier acuity (Fahle & Daum, 1997), spatial interval (Latham & Barrett, 1998), luminance-defined shape (Sara & Faubert, 2000) and luminance-defined spatial frequency information (Faubert & Bellefeuille, 2002; McIntosh, Sekuler, Penpeci, Rajah, Bennett, Grady, & Sekuler, 1999).

We recently conducted two studies looking at the effect of aging on VWM (Faubert & Bellefeuille, 2002; Sara & Faubert, 2000). In both these studies, a particular attention was placed on the control for the sensory input differences between the younger and older observers in an attempt to isolate the WM processes. In the first study, we assessed the ability to detect, discriminate, and store information on object sizes (Sara & Faubert, 2000). In the second study, we evaluated the ability to store spatial frequency information in the presence of interstimulus masks. We further measured VWM for spatial frequency when this information had to be processed within the same attribute (e.g., luminance-luminance or colour-colour) or between attributes (e.g., luminance-colour or colour-luminance).

VWM FOR SIZE INFORMATION

In the Sara and Faubert paper (2000), the sensory, perceptual, and VWM capacity of young and older observers for processing luminance-defined shape

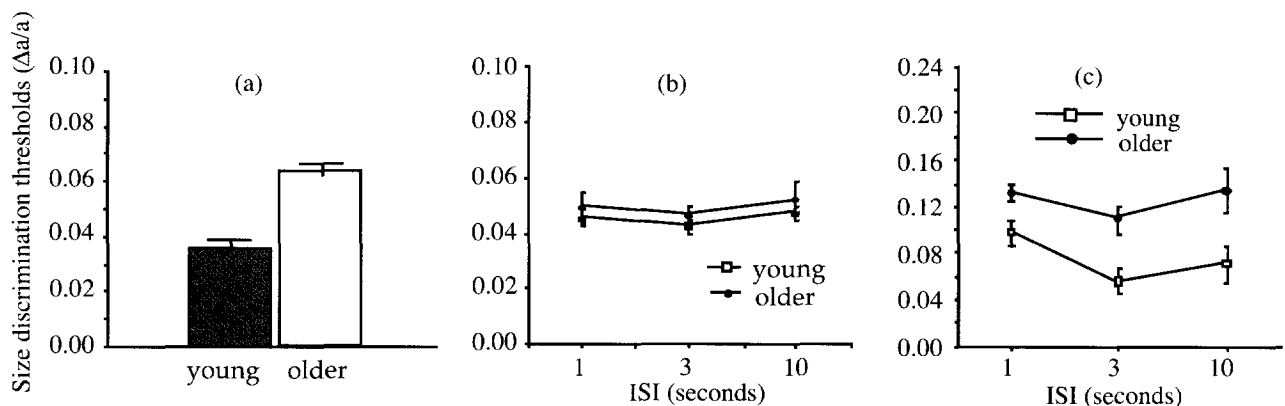


Figure 4. Size discrimination thresholds for young and older observers. (a) Data for simultaneously presented squares. (b) Data for VWM experiments for different ISI conditions. (c) Data for delayed matching task as a function of different ISIs. Error bars are the SEM. Adapted from Sara and Faubert (2000).

information was assessed in a series of experiments. The following were assessed: Each individual's threshold necessary to detect a square from its background as measured by contrast sensitivity; the capacity for making simultaneous size discriminations when compensating for individual differences in sensory input (spatial forced-choice task); the capacity for making sequential size discriminations (temporal forced-choice task); and the capacity for remembering size differences over time (delayed matching task). The results show a selective deficit for simultaneous perceptual processing for older subjects (spatial forced-choice task), which cannot be attributed to differences in sensory input, task difficulty, interhemispheric transfer, or VWM.

We conducted five experiments in this study. The first experiment established the individual luminance contrast thresholds for the luminance-defined squares used throughout that study. The results demonstrated an age-related loss for luminance contrast as expected from previous aging experiments (see Luminance section above). We then used these data to individually compensate for the sensory input in Experiments 2 and 3 by presenting the stimuli at 0.5 log units above each observer's threshold. The results of Experiments 2 and 3 are illustrated in Figure 4a, b. What these data show is that there is a perceptual loss for simultaneous discrimination (Panel a) even if we compensate for the individual sensory differences. The data further show that with the same compensation, there is no loss of VWM for size discrimination (Panel b).

The same control for individual differences in sensory input was used in Experiments 4 and 5. In Experiment 4, two squares of different sizes were presented simultaneously, but in this case the subjects had to determine whether a third square, presented at different ISIs, was the same size as the initial square pre-

sented to the left or to the right (delayed matching task). The results show that when we use a delayed matching task, the results are the same as those found for the spatial forced-choice task (Experiment 3) and they do not change as a consequence of ISIs. The loss is incurred at the perceptual level when the two squares to store in WM are initially processed (see Figure 4c). Experiment 5 confirmed that the simultaneous perceptual processing deficit was not an effect of stimulus configuration (i.e., not a consequence of interhemispheric transfer, for instance). We did this by conducting a spatial forced-choice task when the stimuli were vertically positioned (one above the other) in the left hemifield, right hemifield, or at the vertical midline. The results were identical to Experiment 3 when the squares were separated within the horizontal axis.

These results are particularly interesting because they demonstrate that there is something particular about simultaneous form processing at the perceptual level. As it will be elaborated further in the discussion, I propose that simultaneous perceptual processing may represent a particular case of complex perceptual processing and therefore emphasize age-related losses.

VWM FOR SPATIAL FREQUENCY INFORMATION

In the Faubert and Bellefeuille (2002) study, we wanted to assess whether a memory mask and aging would interact in the retention of spatial information in VWM. We also wanted to explore VWM and processing complexity in young and older observers by using different attributes to define spatial frequency information.

It is possible that the lack of aging effects on VWM shown in previous studies (e.g., McIntosh et al., 1999; Sara & Faubert, 2000) are due to the low-level nature of spatial frequency and luminance processing. One way to disrupt this processing is by using masking

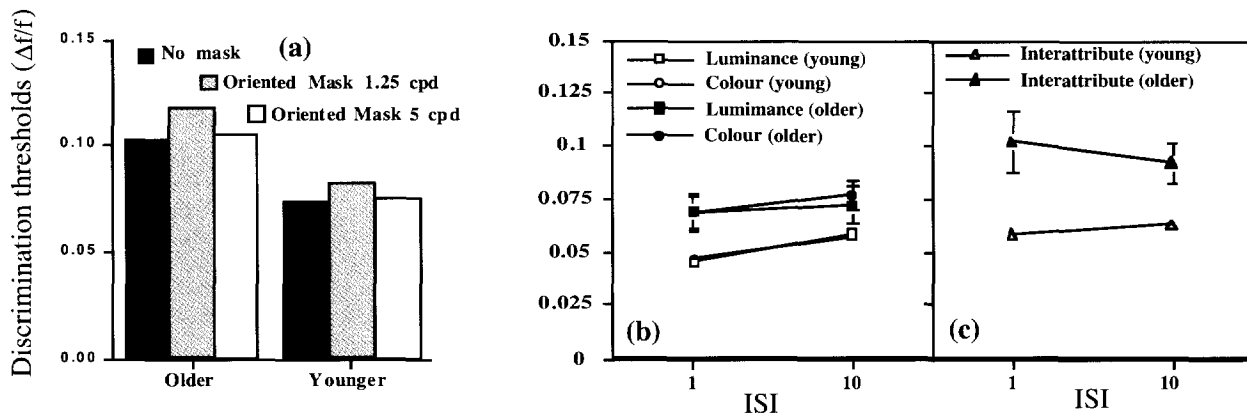


Figure 5. Spatial frequency discrimination thresholds for young and older observers. (a) Data for VWM experiment in the presence of masks. (b) Intraattribute condition data for VWM experiments. (c) Interattribute condition data for VWM experiments. Error bars are the SEM. Adapted from Faubert and Bellefeuille (2002).

stimuli during the retention task (Magnussen et al., 1991). The first experiment tested older versus younger observers in their capacity to retain spatial information while in the presence of a mask stimulus during retention. Prior to testing, individual differences for detecting the stimuli and masks were evaluated by contrast sensitivity. These differences were compensated for in the same way as in the Sara and Faubert study (2000) by using stimuli presented at 0.5 log units above individual thresholds.

We found that the addition of a memory mask during the retention interval did not significantly affect retention capacity (see Figure 5a). In our task, subjects had to report the orientation of the mask ensuring that the stimulus was encoded. Magnussen and colleagues demonstrated that mask orientation did not have an effect on performance so our differences should not be attributed to orientation. Therefore, either the mask orientation does have an effect on masking or the masking effects observed in these types of stimuli are not very robust. The later explanation would argue against a low-level encoding model for VWM of spatial information. Other researchers have also failed to report masking effects on VWM experiments. For instance, Thompson, Stone, and Walton (1996) reported failure to replicate masking effects with velocity judgments for motion stimuli unlike what was reported by Magnussen and colleagues (Magnussen et al., 1992).

Our results agree with other studies on aging and VWM for simple visual attributes that report no loss of information for vernier acuity (Fahle & Daum, 1997), spatial interval (Latham & Barrett, 1998), luminance, defined squares (Sara & Faubert, 2000) and luminance, defined spatial frequency information (Bennett et al., 2001; McIntosh et al., 1999).

Faubert and Bellefeuille (2002) also assessed whether

aging had an effect on the capacity to retain spatial information between different attributes. Assuming that these attributes are initially processed separately and then compared at a higher level (Cavanagh, 1988), we may expect a larger deficit from aging under these conditions due to an increase in processing demands.

In the first condition, the reference and comparison stimuli were both defined by luminance (LL condition), whereas in the second condition, the reference and comparison stimuli were both defined by colour (CC condition). In the third condition, (interattribute condition), the reference and comparison stimuli were respectively defined by a different attribute (colour-luminance or luminance-colour).

The results of this experiment indicate that there is no loss of spatial frequency information with a delay of 10 seconds, regardless of the defining attribute. Thresholds obtained when the stimuli were defined only by colour, CC condition, were very similar to the ones obtained with luminance-defined stimuli (LL), as shown in Figure 5. We also measured spatial frequency discrimination when the stimuli were defined by two different attributes (interattribute). Thresholds in the interattribute condition were significantly higher than in the LL and CC conditions but did not change over the 1- and 10-second intervals. The elevation in thresholds obtained in the interattribute condition, relative to the luminance and colour conditions in younger subjects, suggests that this condition is more complex, thus requiring more processing resources. Our data clearly show that the older observers are more affected in the interattribute condition. These data are interesting in the sense that the larger age-related effect seen in the interattribute condition supports the hypothesis that perceptual losses due to aging should be more apparent when processing complexity increases. In

this case, spatial frequency information has to be processed by two different visual attributes (colour and luminance) before they can be compared to one another. This inevitably requires more processing (more complex network) as evidenced by the increased thresholds for the younger observers in these conditions.

General Discussion

Recently, a series of functional imaging studies have been conducted examining the cortical activation of young and older observers for spatial memory tasks, similar to Experiment 1 of the Faubert and Bellefeuille study (Bennett et al., 2001; Della Maggiore et al., 2000; Macintosh et al., 1999). They found no effect of aging on the psychophysical performance for retaining spatial frequency information much like our own results. What is interesting in those studies is that they found that the neural substrates involved in performing these tasks were different between older and younger observers even if behavioural performance was identical for both groups. They suggested that this reorganization of the older brain may be the consequence of a larger recruitment of neural networks required to perform a given task, which has become necessary to compensate for weakened areas. This proposition is in accordance with the processing complexity hypothesis of aging and may shed light as to why older observers do not show decrements for some low-level memory tasks. It is conceivable that the alternate neural circuits available are limited and that simple memory tasks may not saturate these alternatives. However, if a task is made more complex, the compensatory "neural routes" required to perform this task in the aging brain should increase in a nonlinear fashion where a level of saturation can rapidly be reached. The study by Habak and Faubert (2000) was based on this rationale. We argued that processing of a second-order stimulus should be more affected by aging than a first-order stimulus. The argument was based on the fact that processing second-order stimuli requires larger neural networks and the consequences of aging would be more detectable under these conditions. Evidence that second-order stimuli require more processing comes from psychophysical modeling and fMRI studies. Models developed to explain processing of second-order stimuli always imply additional processing stages to extract visual features (Clifford & Viana, 1999; Wilson, 1998) and the fMRI studies showed that second-order processing implicated additional brain areas as compared to first-order processing (Smith et al., 1998). For instance, the first-order motion stimuli would primarily activate V1 and V5 while the second-order motion stimuli would activate other extrastriate areas such as V3 and V4 in

addition to V1 and V5.

The functional imaging studies on visual working memory mentioned above may also shed light on the Sara and Faubert (2000) study. When the same size judgment had to be made from simultaneously presented squares, a significant loss of aging was observed even if there were no age effects when the same judgments were made sequentially (VWM). This led us to speculate that, if the neural networks required to process the size of two squares had to be accessed simultaneously, any weakness of the circuit would become more obvious. Alternatively, if the compensating neural circuits can be accessed in alternation (first square stored then compared with the second), the evidence of a weakened neural circuit may be less evident, even if the sum of the sequentially accessed circuits may involve a larger total network than when the two squares have to be accessed simultaneously ("simultaneous access deficit" hypothesis).

In conclusion, we have shown a wide range of deficits due to aging but we have also demonstrated that the magnitude of these age-related changes essentially depends on the stimulus complexity (computational load or complexity of neural network). For instance, in the motion and texture tasks in the Habak and Faubert (2000) study, the perceptual loss due to aging was clearly more evident in the second-order motion and texture tasks as opposed to the first-order motion and texture tasks. It is generally accepted now that the second-order tasks require more processing and, in fact, involve more brain areas to be perceived (Clifford & Viana, 1999; Smith et al., 1998; Wilson, 1998). We showed that for colour-defined motion (a first-order attribute), there was no effect of aging when sensory input differences are compensated for. Aging also diminishes bilateral symmetry detection, a task assumed to require mid-level processing for the types of stimuli we used (Barlow, 1978; Barlow & Reeves, 1979). We also showed dramatic effects of aging when size discrimination for two squares had to be done simultaneously or when spatial frequency information for two gratings had to be transferred from one attribute to another for comparison (e.g., colour to luminance). As argued above, both of these conditions are presumed to require more complex neural networks. Finally, VWM for low-level spatial information appears unaffected by aging when individual differences of sensory input are compensated for. However, many studies have shown that more complex memory tasks (e.g., dual attention tasks; see Craik & Jennings, 1992) are affected by aging.

Although the psychophysical response for a perceptual or VWM task with low-level stimuli may not be affected, it is not to say that there is no underlying

change in the neural networks required to process such information in the older individuals. The functional imaging studies clearly demonstrate that changes have occurred in the neural circuitry involved but they may not have reached a point of saturation when simple stimuli have to be processed. When more complex networks have to be accessed, either by way of simultaneous processing or when the stimuli are perceptually more complex, such as in second-order stimuli conditions, or when more than a single attribute must be processed to make a decision, the underlying dysfunction may become more obvious and could be expressed by functional deficits.

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