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Field of View, Figure/Ground Discrimination, Sequential Memory, and Navigation Skills Improve Following Training on Motion Discrimination in Older Adults

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ABSTRACT

Background: Brain timing is disrupted in older adults affecting attention, memory, navigation and mental processing speed. Processing speed deficits, in turn, are thought to underlie older adults' decline in cognitive capabilities. Moreover, older adults have decreased contrast sensitivity for motion detection and discrimination. These contrast sensitivity losses are likely due to age-related changes in magnocellular pathways. Previous studies of older adults found that training on motion detection and discrimination, combined with object recognition, significantly improved processing speed and navigation.

Methods: This pilot study addressed whether training on direction discrimination, which improves timing in the dorsal pathway, would improve the ability of older adults to discriminate the direction of motion and increase mental processing speed, thereby improving visual and higher cognitive functions, like driving, navigation, and sequential processing. Seven adults between the ages of 55 to 74 were studied. In this study, each person completed two sessions of direction-discrimination training (20 minutes or less) twice a week for an average of 12 weeks, using patterns optimized for activating magnocellular pathways.

Results: Across all subjects, direction discrimination contrast sensitivity improved significantly ($p<0.0001$), an average of 7-fold. Among other symptoms, the older adults in this study reported difficulties when driving. In hindsight, these reported driving difficulties appear to be related to a decreased useful field of view. Following training on direction discrimination, observers reported that these limitations were resolved. These older adults found an increase in their functional field of view, better figure/ground discrimination, enhancements in working memory, sequential processing, and improvements in navigation.

Conclusions: It is possible that the deficits in attentional focus, figure-ground discrimination, sequential memory, and navigation experienced by some older adults result from an information overload due to timing deficits that are abated following training on direction discrimination. One possible neurobiological mechanism for these timing deficits of older adults is that sluggish magnocellular neurons found in the dorsal pathway do not signal in advance of the parvocellular neurons, making it difficult to attend in direction discrimination tasks.

Keywords: Attention gateway, cognitive aging, contrast sensitivity, cortical plasticity, magnocellular pathways, motion discrimination, navigation, parvocellular pathways, perceptual learning, sequential memory, speed of processing, timing

Introduction

As people age, some brain functions are diminished, especially speed of processing information.[1-3]

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In the interest of full disclosure, it should be noted that Dr. Lawton has a significant financial interest in many of the topics/therapies discussed in this article.

Lawton T. Field of view, figure/ground discrimination, sequential memory, and navigation skills improve following training on motion discrimination in older adults. Optom Vis Dev 2009:40(2):82-93.

Processing speed deficits are thought to underlie the cognitive decline found in older adults.[4,5] Moreover, the prevalence of speed of processing deficits increases with age.[6] For older adults, training using motion detection and discrimination combined with object recognition[7-11] significantly improved processing speed and performance in driving and other mobility and navigation tasks.

There is fMRI evidence that the posterior portion of the older brain, such as cortical areas V1 and MT show less activation than do their younger counterparts.[12] In addition, older adults have a decreased sensitivity to radial motion, i.e. optic flow, analyzed in cortical area MST, that is directly related to impaired navigational skills.[13] Moreover, behavioral data using careful psychophysical techniques show adults over 50 have decreased contrast sensitivity to vertical sinewave gratings at low spatial frequencies[14-18] under photopic, mesopic, and scotopic viewing conditions. These contrast sensitivity losses are likely due to age-related changes in magnocellular pathways.[18] Children also show this decreased contrast sensitivity to stationary patterns[19,20] and patterns moving relative to a textured background.[19-22] Furthermore, training on left-right movement discrimination significantly and rapidly improved children's contrast sensitivity for movement discrimination[19-22] as well as higher cognitive functions, e.g. their reading skills.

This pilot study determined whether training on direction discrimination would improve the ability of older adults to discriminate the direction of motion and speed of processing, thereby improving visual and higher cognitive functions. For older adults, training on a motion discrimination task (juggling) increased gray matter in both cortical area MT and the hippocampus.[64] Direction-discrimination training provides a much simpler and more rapid paradigm for improving speed of processing than previously used treatments.[11,23,24] The older adults in this study reported that in the past they had experienced a decreased useful functional field of view when driving. Furthermore, they also reported a decrease in their field of view when engaged in working memory tasks, e.g. in their employment. As they aged, a narrowed field of view was the primary way to focus their attention, thereby reducing the effort needed to complete a task by limiting the amount of information to be processed. With training, these older adults found their usable field of view improved,[11,23] thus enabling them to see much more in a single glance and with much more clarity. They also experienced better figure/ground discrimination, and improvements in navigation, e.g. driving in general, but more so when driving at dusk and at night. Working memory was reportedly improved by all subjects, thus reducing confusion on the job and the ensuing stress associated with information overload.

Methods

Subject Selection

The second author administered a vision questionnaire, adapted from the Low-Luminance Questionnaire,[65] to determine who was at risk for having problems with motion discrimination (see Table 1). As a result of their responses, seven older adults, aged 55 to 74, were recruited to participate in this study. Their motion discrimination deficits were verified by psychophysical measurements using the first session of PATH therapy. All subjects had visual acuity correctable to 20/20, and had age appropriate ocular media changes.

PATH to Reading Therapy: Left-Right movement discrimination

PATH to Reading,[19] uses displays (see Figure 1) comprising a stationary, central, "fish-like" window surrounded by a stationary, vertically oriented sinewave grating of spatial frequency $w_{background}$. The fish-like window contains a vertical test sinusoid of spatial frequency w_{test}. A given trial comprises three frames, each lasting 150 ms for the first 4 levels of complexity, listed in Table 2. The phase of the test grating on frame 1 is ±45° chosen randomly. On each of frames 2 and 3, the test grating shifts 90° (1/4 of a cycle) in a fixed direction (either rightward or leftward), and the task of the trainee is to indicate the direction of movement using the right or left arrow keys. A brief tone is presented after incorrect responses.

The protocol for training left-right movement discrimination was:

1. Left-right direction discrimination of a sinusoidal test pattern moving relative to a sinusoidal OR a multifrequency background pattern, since multifrequency backgrounds have been shown to increase the range of discriminable patterns at very low contrasts. [25,26]
2. Five percent background contrast for single and multifrequency gratings, with 10%, and 20% background contrasts for multifrequency

Table 1. Low Luminance Questionnaire

Please answer the questions as if you were wearing your glasses or contact lenses (if any). Choose the response that best describes your situation at this time. The answers are as follows: N = Never (0-24%), S= Sometimes (25-49%), O= Often (50-74%), and A= Always (75-100%).

1. I have difficulty seeing in bright sunlight.	N S O A
2. I find fluorescent lighting irritating, especially if one of the tubes is flickering.	N S O A
3. I have difficulty seeing people's faces in a hallway when there is light coming from behind them.	N S O A
4. I have difficulty reading menus in a dimly lit restaurant.	N S O A
5. I have difficulty reading the newspaper w/o good lighting.	N S O A
6. I have difficulty seeing while driving in the rain.	N S O A
7. I have difficulty seeing while driving at dusk or at night.	N S O A
8. I have difficulty reading print on dark colored paper.	N S O A
9. I have difficulty seeing dark colored cars at night.	N S O A
10. I have difficulty moving about in a darkened theater.	N S O A
11. I have difficulty going out for night-time social events such as church, theater, friends' home, etc.	N S O A
12. I depend upon others to help me see under low light conditions or in the dark.	N S O A
13. I am worried about taking a fall because of my balance or how I see things in my path.	N S O A
14. I tend to be clumsy under low light conditions.	N S O A
15. I have difficulty with depth perception at night.	N S O A
16. I have difficulty deciding how much brake pressure to apply, because of how I judge where I am in space.	N S O A
17. I have difficulty with my peripheral vision under poor lighting conditions or at night.	N S O A
18. I have difficulty reading street signs while driving at night.	N S O A
19. Oncoming headlights bother me at night.	N S O A
20. I limit my nighttime driving because of how I see.	N S O A
21. Glare at dusk or dawn bothers me.	N S O A
22. I feel bad or depressed because of how I see at night or under poor lighting conditions.	N S O A
23. I have taken a fall and hurt myself.	N S O A
24. I am worried about my risk of taking a fall.	N S O A.
25. I am having difficulty with my memory.	N S O A
26. I limit my freeway driving.	N S O A
27. I tend to have attention problems or zone out at times.	N S O A
28. I tend to have unexplained blurry vision or tunnel vision at times.	N S O A
29. I lose attention when reading print for more than 30-45 minutes.	N S O A
30. Certain wallpaper or fabric makes me feel dizzy or annoyed.	N S O A

gratings, the background contrast increasing when the previous level of complexity (Table 2) was learned.

3. Test pattern spatial frequencies of 0.25, 0.5, 1, and 2 cycles per degree.
4. A test pattern speed of 6.7 – 13.3 Hz. The pattern moves ¼ cycle, or 90 degrees, in the same direction every 150 msec – 75 msec at different levels of complexity, see Table 2. This creates the perception of leftward or rightward movement.
5. Sinusoidal background patterns of different spatial frequencies, ranging from two octaves below the test pattern to two octaves about the spatial frequency of the test pattern, each background frequency being an octave apart, since neurons in the direction-selectivity network are tuned to approximately one octave.[27,28]

At the start of a session, both the test and background gratings were set to 5% contrast, to ensure the pattern's contrast is in the middle of the magnocellular contrast range.[29] Each time the subject correctly identified the direction the fish stripes moved, the contrast of the test grating was lowered until the subject made an incorrect response. The step size varied from 0.3% down to a step size of 0.1% at 0% contrast. Very low contrasts were obtained by special modifications to the computer's color lookup table, varying only one color gun at a time. Although these manipulations might be expected to lead to hue heterogeneities in the stimuli, they are not visible, and moreover, it is well documented that judgments of motion direction in very low contrast stimuli depend only on luminance variations.[30] Following the first incorrect response, a double-staircase procedure[31] was used to estimate the direction discrimination contrast thresholds. Three successive correct responses reduced test grating contrast by one step; each error increased the test grating contrast by one step. The staircase terminated after 6 reversals, and the mean of the last 3 was taken to estimate contrast threshold. If the last 3 reversals, where the threshold value should be leveling off, contain 4 or more increments in contrast, the threshold was considered too variable to be reliable, and the contrast threshold was automatically re-measured by the computer. Using the last 3 of 6 contrast reversals was found previously[31] to provide the most reliable results compared to using larger numbers of contrast reversals. This staircase procedure estimates the contrast needed for 79% correct responses. Each session took about 10 minutes to complete. At the end of each staircase run, the trainee received a score to increase motivation: The lower the contrast threshold, the higher the score. All PATH therapy was administered by the second author's vision therapist.

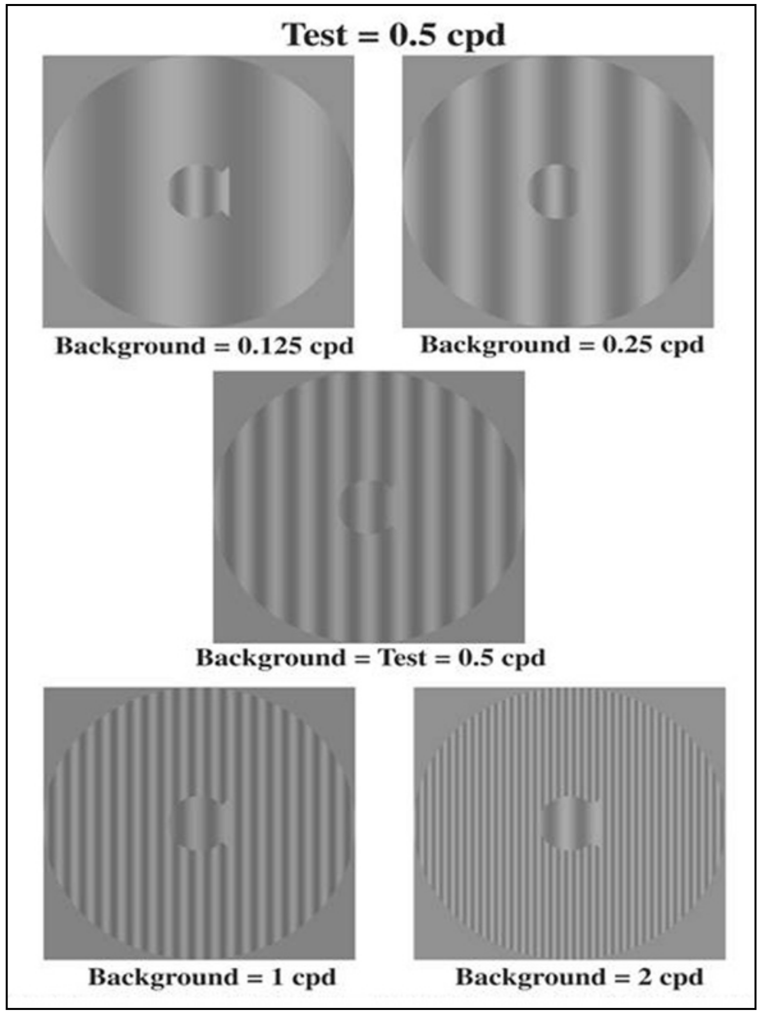

Figure 1: *Sample Patterns for test frequency = 0.5 cyc/deg (cpd) on different backgrounds.*

In a given staircase run, the center spatial frequency, w_{test}, was either 0.25, 0.5, 1, or 2 cyc/deg, and the surround grating spatial frequency, $w_{background}$, was either equal to the test frequency or 1 or 2 octaves higher or lower. A full training cycle of the left-right movement discrimination task required 20 threshold determinations (*i.e.* one for each of the four test spatial frequencies paired with each of the five background spatial frequencies, progressing from 2 octaves below to 2 octaves above the test spatial frequency). Each

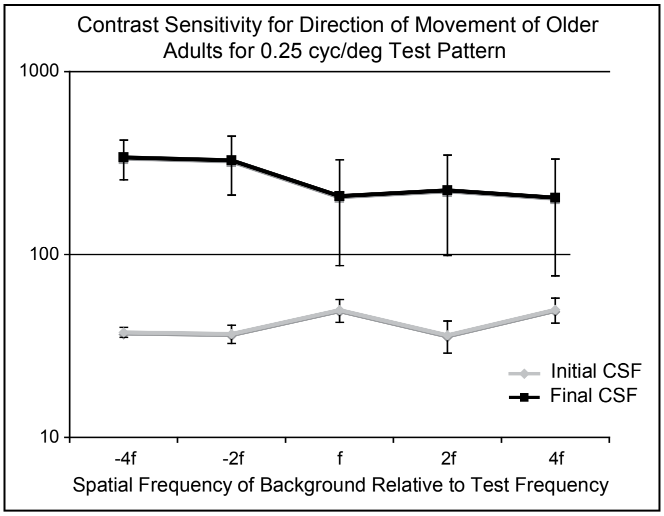

Figure 2a

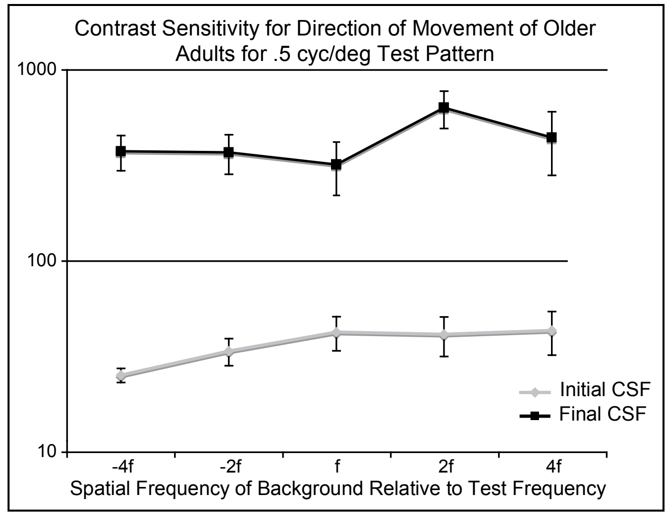

Figure 2b

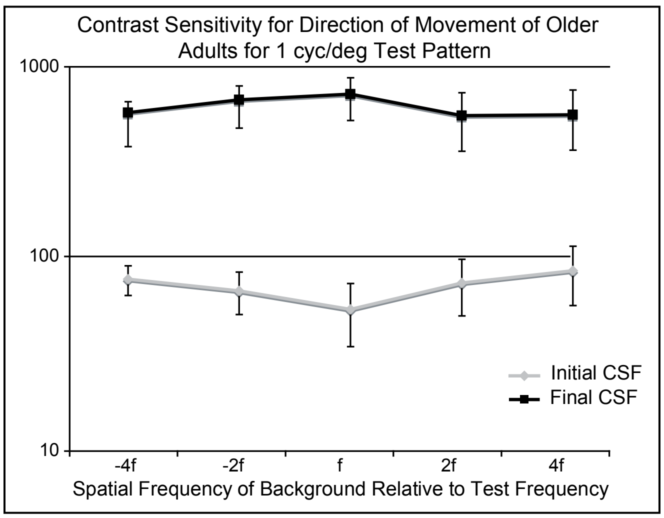

Figure 2c

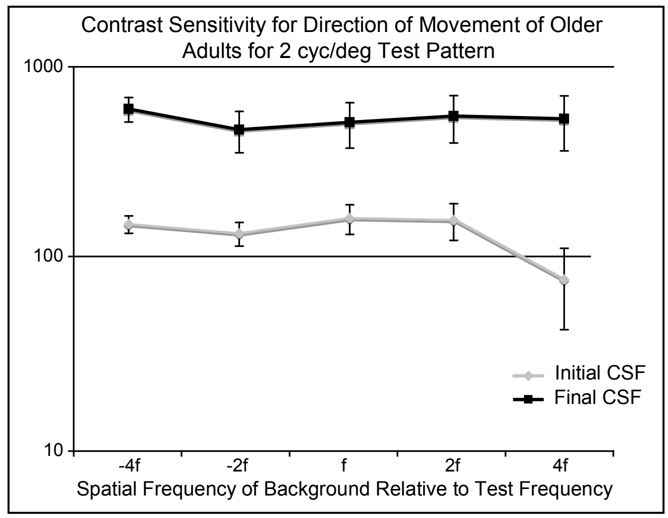

Figure 2d

Figures 2a-d: *Contrast Sensitivity Functions (CSF) at the beginning and end of PATH to Reading training for each test pattern, 0.25 (Fig. 2a), 0.5 (Fig. 2b), 1 (Fig. 2c) and 2 cyc/deg (Fig. 2d).*

session covered half a training cycle, consisting of 10 threshold determinations: one threshold for each of two 'test' frequencies displayed within each of five background frequencies. In the first session, all thresholds involving test spatial frequencies 0.5 and 1 cyc/deg were measured. In the second session, all thresholds involving test spatial frequencies 2.0 and 0.25 cyc/deg were measured. All subjects completed one training cycle (two sessions) each time they were trained.

In addition to the sinewave backgrounds, multifrequency backgrounds were used. For multifrequency backgrounds, the first spatial frequency component is the same as used in single frequency backgrounds. In this manner, multifrequency backgrounds consisting of three spatial frequency components are bootstrapped to the original single frequency background. Bootstrapping is done by adding two higher spatial frequencies to the first, each of which differs from the previous frequency by an amount equal to the test frequency. This bootstrapping method insures that the background has a low fundamental frequency that either 1) equals the fundamental frequency of the single frequency background grating when the spatial frequency of the background is lower than or equal to the spatial frequency of the test frequency, or 2) lowers the fundamental frequency of the background to be equal to that of the test pattern's spatial frequency when the first background frequency component is higher than the test frequency. For example, when the sinewave background for a 1 cyc/deg test pattern is 4 cyc/deg (the one that is two octaves higher than the test frequency), then the fundamental frequency (greatest common denominator) of the 4+5+6 cyc/deg multifrequency background, is lowered from 4 cyc/deg (sinewave background) to 1 cyc/deg (multifrequency background). Adding in higher background frequencies that lower the background's fundamental frequency, for backgrounds higher in frequency than the test frequency has been shown previously to improve the contrast sensitivity for movement discrimination over a wider range of different backgrounds than found using single frequency backgrounds.[25,26]

Initially, three consecutive 150 msec time intervals were used to present leftward or rightward movement to ensure that 1) a long duration dynamic stimulus was used and 2) this task was easy for dyslexic readers. Even though apparent motion was used, the motion always appeared smooth because of the fast speeds. When 150 msec intervals are used, the speed of the test pattern has a constant temporal frequency of 6.7 cycles per second (Hz). A constant temporal frequency causes the speed to appear faster for low spatial frequencies which subtend a wider spatial extent (test frequencies of 0.25 cyc/deg), than for higher spatial frequencies which subtend a narrower spatial extent. After each 4 levels of complexity were completed, *i.e.* on the fifth, ninth, and thirteenth levels, see Table 2, the speed of each pattern interval increased by 25 msec, increasing the pattern's temporal frequency up to 13.3 Hz. Not only did the pattern's temporal frequency increase, but the background pattern is now a sine-wave grating, not increasing to a multifrequency background until the next level of complexity. This is done to first train each spatial frequency channel separately, using contrasts optimal for magnocellular processing. Multifrequency backgrounds activate additional spatial frequency channels, increasing the activity of cortical processing. Increasing the contrast of these backgrounds increased the activity of parvocellular neurons, aiding in the integration of magnocellular and linked parvocellular activity.

The stimuli used for training on left-right direction discrimination (see Figure 1) were previously found to be optimal for measuring the sensitivity of directionally-selective motion pathways.[25,26,31] The procedure for determining optimal activation of directionally-selective motion pathways were as follows:

Table 2. The parameters for each level of complexity:

Complexity Level	Duration of Each Interval	Background Frequencies	Background Contrast
1	**150 msec**	Single frequency	5%
2	150 msec	Multifrequency	5%
3	150 msec	Multifrequency	10%
4	150 msec	Multifrequency	20%
5	**125 msec**	Single frequency	5%
6	125 msec	Multifrequency	5%
7	125 msec	Multifrequency	10%
8	125 msec	Multifrequency	20%
9	**100 msec**	Single frequency	5%
10	100 msec	Multifrequency	5%
11	100 msec	Multifrequency	10%
12	100 msec	Multifrequency	20%
13	**75 msec**	Single frequency	5%
14	75 msec	Multifrequency	5%
15	75 msec	Multifrequency	10%
16	75 msec	Multifrequency	20%

1. Sinewave gratings (activating both low and high levels in the motion pathways) were used, instead of random dots that activate only high levels in the motion pathways.[32] Perceptual learning is over 10-fold faster when discriminating the direction of sinewave gratings[33] than for random dot patterns.[3]
2. The test sinewave grating moved 90 degrees (deg) between the first and second pattern interval, since this is the optimal phase difference for direction discrimination.[31]
3. A range of test frequencies (0.25, 0.5, 1, and 2 cyc/deg) was used to span the spatial frequencies that predominantly activate motion pathways.[27,29,34]
4. A 4-octave range of clearly visible background spatial frequencies, set to 5% contrast, centered around the test spatial frequency was used to map out each channel's spatial frequency tuning function. These background frequencies are an octave apart, since neurons in the direction-selectivity network are tuned to approximately one octave,[27,28] and perceptual learning of direction discrimination does not transfer to spatial frequencies differing by more than one octave[33]. Increasing the background structure by using multiple spatial frequencies, having a low fundamental frequency, increases the contrast sensitivity of movement discrimination

Table 3. Proportion Contrast Sensitivity Function (CSF) Improved Following Training

Test Pattern	0.25 cpd	0.5 cpd	1 cpd	2 cpd	Mean
Test = Background (Fig. 3)	4.2	7.5	12.2	3.2	6.8
Mean CSF (Fig. 4)	6.2	11.5	8.0	4.0	7.4

for a wider range of background patterns than found with single frequency backgrounds.[25]

5. Initially, both the test and background sinewave gratings were presented at 5% contrast, so that these patterns would be in the center of the working range of the magnocellular neurons.[29]
6. The Contrast Sensitivity Function (CSF, the inverse of the contrast threshold function) was used to evaluate a subject's direction discrimination ability, since the CSF is most directly related to the output response of a directionally-selective motion cell.[35]
7. To prevent the involvement of saccades, left-right movement was presented by having the test sinewave grating move left or right (determined randomly) in 150 msec pattern intervals, since saccadic programming takes around 150 msec.[36] This design also prevents express saccades[37] from contributing to direction discrimination. This range of temporal frequencies, from 6.7 Hz for 150 msec pattern intervals to 13.3 Hz for 75 msec patterns is centered around the peak temporal frequency of the visual system which is 10 Hz.

There were 16 levels of complexity, as defined in Table 2. The level of complexity did not increase until the mean contrast threshold of the 2 cyc/deg test pattern, the pattern subjects were most sensitive to its direction of movement, also seen in Figures 2 and 3, was less than 1% contrast. The level of complexity was adjusted automatically.

Contrast Sensitivity Functions (CSF) were computed to evaluate the effectiveness of training direction-selectivity. The initial direction discrimination CSF was determined by the contrast sensitivity after completing the first replication. The subsequent CSFs were the maximum contrast sensitivity to discriminate the direction of movement for each test-background pattern combination at each level of complexity, from 1 to 16. The CSF data, stored in individual and summary files, were collected automatically by the computer, which also recorded the level of pattern complexity, and the time used to complete each set of 5 patterns (one-half a session). The patients averaged twelve weeks of direction-discrimination training, each having two sessions twice a week in the second author's office. One patient trained for 16 weeks and two for 11 weeks. The other 4 patients completed PATH to Reading training in 12 weeks. Following the completion of training, the first author conducted interviews with each subject in this study to assess their improvements in reading, figure/ground discrimination, sequential memory, field of usable vision, and ability to navigate. Each subject was asked to report any changes they had noticed since direction-discrimination training began.

Results

Contrast Sensitivity for Direction Discrimination (PATH to Reading program)

The low initial Contrast Sensitivity Functions (CSF) improved significantly following direction-discrimination training, see Figures 2a-d. Following direction-discrimination training, each subject's CSF improved an average of 7 fold, see Table 3. Except for the large jumps in CSF at the beginning and end of the training, the improvements in CSF were gradual as shown in Figures 3 and 4. When analyzed using a two-factor ANOVA, $F(16,3) = 18.02, 83.8$, $p < 0.00001$, each person's CSF improved significantly over the course of training for each of the four test frequencies. This high level of significance shows that 7 subjects were sufficient to generate the statistical power needed for this analysis. In Figures 3 and 4, the initial CSF before training is labeled complexity level 0. Each higher level of complexity corresponds to the level listed in Table 2. Since the CSF is most directly related to the output response of directionally selective motion cells,[66] improvements in a subject's CSF reflect an improvement in the sensitivity of these motion-tuned cells.

Previous data showed that when test and background spatial frequencies were equal, the CSF was lowest for subjects with magnocellular dysfunction and highest for those with no magnocellular dysfunction. Since older subjects were recruited for this study based on exhibiting magnocellular deficits, the graphs for this stimulus combination are plotted in Figure 3. The same pattern of results is found when the mean CSF was taken over all five background

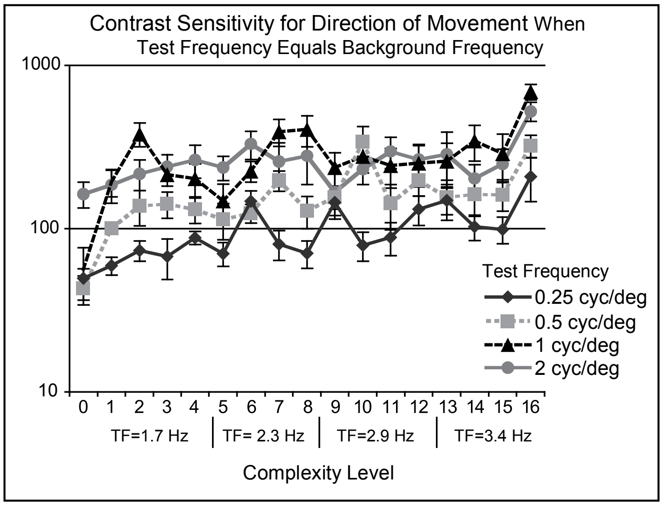

Figure 3: *Contrast sensitivity for direction of movement when test frequency equals background frequency for each test frequency, when averaged across subjects.*

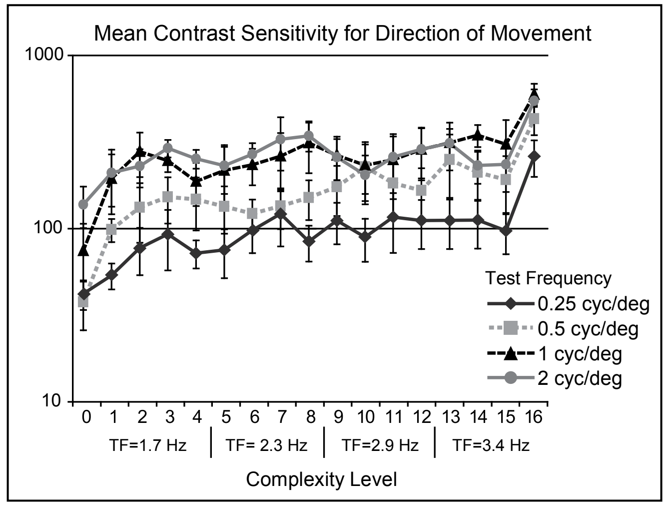

Figure 4: *Mean contrast sensitivity function for direction of movement for each test frequency, when averaged across subjects.*

spatial frequencies, as shown in Figure 4. The major difference between the two figures is that the curves for the 1 and 2 cyc/deg test patterns are more closely aligned when examining the mean CSF (Figure 4).

It is striking that the largest jump in sensitivity occurs initially and at the highest level of complexity. It is likely this occurs initially, because the timing in the dorsal pathway is changing. Furthermore, it is likely this occurs at the highest level, since this stimulus combination maximizes interactions between magnocellular and parvocellular pathways, having the fastest temporal frequency, 13.3 Hz, and highest background contrast, 20%. Subjects reported that each time they did the direction-discrimination training; they noticed concomitant improvements in the usable field of view and the saliency of improved figure-ground discrimination, as well as their ability to remember and navigate. Moreover, the CSF for each of the test frequencies shows that the direction of movement of 1 and 2 cyc/deg patterns are seen most easily, having a higher CSF across complexity levels. Subjects required more contrast to discriminate the direction of movement between test patterns below 1 cyc/deg, the lowest spatial frequency tuned channel found in people,[38] with the lower the test frequency, the more contrast that was needed, see Figures 3 and 4. In fact, the CSF improved the most for the 1 cyc/deg test pattern initially, and over the course of training when test and background frequencies were equal, as shown in Table 2. It is likely that discriminating the direction of movement for bars wider than 1 cyc/deg required pooling information across channels tuned to a range of spatial frequencies. Subjects all found discriminating the direction of 0.25 cyc/deg test patterns hardest to do initially and easiest after the first month of direction-discrimination training. However, the CSFs were always lowest for the 0.25 cyc/deg pattern as seen in Figures 2a, 3 and 4, showing that the visual system is less sensitive to the motion of very low spatial frequency patterns, in older adults.

Improvements in Usable Field of View, Figure/Ground Discrimination, Working Memory, and Navigation

All subjects reported they noticed improvements in their functional field of usable vision, figure-ground discrimination, working memory, and navigation (especially at night after the first month). These responses were provided when asked to report any changes they had noticed since starting their direction-discrimination training, for example, in their vision, memory, or ability to drive, and were not the result of asking specific questions. In addition, these tasks now required much less effort. Moreover, for all subjects, none of these improvements have regressed over time.

Discussion

Following direction-discrimination training for 10-20 minutes twice a week, an observer's contrast sensitivity to detect the direction of movement improved significantly. Moreover, subjects reported that they were able to take in a wider field of view, had improved figure-ground discrimination, working memory, and navigation. Experience refines the output of cortical circuits by introducing patterned activity that fine-tunes the strength of neuronal connections within and among cortical columns.[39] These results are consistent with the hypothesis that the deficits in attentional focus, working memory, and navigation experienced by some older adults result from an information overload due to timing deficits in the direction-selectivity network that is abated following training on direction discrimination. Moreover, these results support the hypothesis that magnocellular pathways provide the gateway for attentive processing.[22]

Movement discrimination most likely tunes the V1-MT loop in the cortex.[19-22] Recent studies found that training on left-right movement discrimination (PATH to Reading therapy), which works by tuning neural brain timing in the dorsal pathway, conveyed predominately by magnocellular neurons,[19-22] improved reading skills 1 to 3 grade levels. We reasoned that if older people who have problems with movement discrimination were trained using PATH therapy, then problems with visual memory and navigation, also conveyed by the dorsal pathway, MT being a key center for these activities, should be alleviated. This hypothesis is strengthened by finding that after a short amount of training, discriminating the direction of movement significantly improved each older subject's ability to navigate, as well as improving working memory, figure-ground discrimination, and usable field of view.

Since this was a pilot study, control groups and pre- and post-tests for the different aspects of attention, processing speed, working memory, and usable functional field of view were not used. Future studies will employ a much larger sample size, control groups, and careful tests of these skills of executive control using the Attention Network Test,[67] the Test of Variables of Attention (TOVA), or Integrated Auditory Visual Attention test (Brain Train), as well as standardized tests of working memory, such as the Stroop test, and field of usable vision, such as automated perimetry with spatially-localized sinewave grating targets, in addition to tests of static contrast sensitivity. These pre- and post-tests will provide objective measures of the skill improvements reported by subjects in their interviews with the first author. Control groups using other interventions will also be employed.

Underlying Mechanisms

One possible neurobiological mechanism for the timing deficits experienced by these older adults is sluggish magnocellular (motion) neurons found in the dorsal pathway, including the LGN and cortical areas V1 and the Medial Temporal (MT) cortex, make it difficult to attend in direction discrimination tasks, since magnocellular neurons would not signal in advance of the linked pattern or parvocellular neurons.[22] It is likely that the ability of magnocellular neurons to bracket the activity of linked parvocellular neurons over time is what has been disrupted, resulting in temporal and spatial sequencing deficits that cause navigation to be more difficult and causes a reduction in the field of view. Since physiological data demonstrate that magnocellular neurons control the gain of the direction-selectivity network,[28] it is plausible that the older subject's more sluggish, immature magnocellular neurons, as shown in this and previous studies[19-22] might be causing a deficit in attentional focus, preventing the linked parvocellular neurons from isolating and sequentially processing the relevant information needed[22,48,49] when navigating, especially at night (low light levels) and under stress (more effort needed to complete the task).

It has been proposed that visual-memory traces are located in the temporal lobes of the cerebral cortex, as electric stimulation of this area in humans results in recall of imagery.[40] Lesions in this area also affect recognition of an object after a delay, in both humans[41,42] and monkeys[43-45], indicating a role in the working memory of images.[46] Shape-selective neurons were found in an anterior ventral part of the temporal cortex of monkeys that exhibited sustained activity during the delay period of a visual short-term memory task.[47] This activity was highly selective for the pictorial information to be memorized and was independent of the physical attributes such as size, orientation, color or position of the object. These results suggest that pictorial working memory, as needed for navigation, is coded by temporary activation of an ensemble of neurons in the region of the association cortex that processes visual information, rather than by neuronal activity in a brain area specialized for short-term memory tasks.[47] Visual working memory is needed for navigation and driving, a task that some find much more difficult as they age.

Neurons with memory-related responses have been reported in multiple brain regions, for example, the posterior parietal and inferior temporal cortices, which are the end stages of the dorsal and ventral visual pathways, respectively.[50,51] The dorsal prefrontal cortex is connected with the posterior parietal cortex, whereas the ventral prefrontal cortex is linked to the inferior temporal cortex. On the basis of this organization, Goldman-Rakic[52] proposed that working memory is mediated by the sustained activity of neurons in parallel, distributed cortical networks. FMRI studies have verified the concurrent activation of multiple human brain areas during performance of cognitive tasks that engage working memory, confirming the findings of the monkey neurophysiological studies.[53]

Recent fMRI and PET studies indicate that older adults have more prefrontal activation as a result of expending more effort to complete tasks, when compared to younger adults.[54] Studies describe the increased activity in prefrontal cortex as due to recruiting additional prefrontal regions to prevent the performance of older adults from declining.[55-58] This is supported by finding that prefrontal cortical activity was reduced similarly by aging and by a divided attention task,[59] suggesting that increasing age and effortful cognitive processing put an equal claim on the available attention resources. Practice requiring less conscious processing has been associated with a decrease in frontal activity.[60] Moreover, left-lateralized (ventral) prefrontal activity (encoding information) that is more active than right-lateralized (dorsal) prefrontal activity (retrieving information) in young adults, is equal in older adults[57-59] suggesting more effort must be made by older adults to retrieve information from working memory for higher cognitive processing like navigation.

The increased activity in the dorsal pathways of older adults required to retrieve information is consistent with the timing of magnocellular pathways having degraded over time. This pilot study shows that training on direction discrimination, designed to strengthen magnocellular activity, increased the ability of the dorsal pathway to improve navigation and memory. The association of the severity of white matter lesions in the cortex and cognitive decline are particularly evident on tests measuring attention and processing speed.[54] In addition, it may be that aging causes a decline in frontal inhibitory control over posterior brain regions.[56,58] These studies provide evidence that that in older adults the timing in their brain is disrupted, affecting attention, processing speed, memory, and navigation. Processing speed and attention have been found to explain a large part of age-related memory deterioration.[61,62] Reduced information processing speed may explain problems in memory encoding and retrieval because this mental slowing can lead to superficial processing and inefficient strategies where elaboration is required.[63] Future research will investigate further whether degradation of the timing and sensitivity in magnocellular pathways underlies age-related reductions in information processing speed using a controlled validation study as described above.

Acknowledgements

This research was funded jointly by Perception Dynamics Institute (PDI) and Douglas W. Stephey, OD, MS. PDI has developed and is marketing the PATH to Reading program (www.pathtoreading.com) based on the clinical techniques described in this paper. It is available worldwide from PDI for vision and educational therapists, and for schools from Early Childhood Parenting Institute, a nonprofit, tax-exempt corporation. Dr. Stephey has no financial interest in PDI.

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