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Neural Correlates of Age-related Reduction in Visual Motion Priming

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Abstract

Previously we reported that priming of visual motion perception is reduced in older adults compared to younger adults (Jiang, Greenwood, & Parasuraman, 1999; Jiang, Luo, & Parasuraman, 2002b). To examine the neural mechanisms underlying this age-related effect, event-related brain potentials (ERPs) were recorded during perceptual judgments of motion directions by younger and older adults in two experiments. When judging single-step motion, both younger and older adults evoked significantly larger ERP late positive component (LPC) responses to unambiguous motion compared to LPC responses elicited by ambiguous motion. In contrast, compared to the younger adults, the older adults evoked comparable but delayed ERP responses to single motion steps. In the second experiment the younger and older groups judged the directions of two successive motion-steps (either motion priming or motion reversals). Under short (200–400 ms) stimulus onset asynchrony (SOA), the difference between the ERP responses to priming and reversal conditions was significantly larger for the younger than for the older adults. This study provides the first electrophysiological evidence that brain aging leads to delayed processing of single motion direction and visual motion priming as early as 100 ms in the early visual cortex. Age-related changes in strength and temporal characteristics of neural responses in temporal-parietal regions were particularly pronounced in older adults when successive motion signals are placed closely in time, within 400 ms.

Keywords

Ambiguous motion; Age-related difference; Bi-stable perception; EEG/ERP; Visual motion priming; Motion reversal

INTRODUCTION

Cortical dysfunction due to brain aging may be an important source of increased risk of traumatic injury for older adults, especially during visually guided activities such as driving and walking. Previous findings indicate age-related deficits exist in detecting motion and in determining motion speed and direction (e.g., Andersen & Atchley, 1995; Gilmore et al., 1992; Norman et al., 2003; Snowden & Kavanagh, 2006; Trick & Silverman, 1991; Warren et al., 1991), motion discrimination (Bidwell, Holzman, & Chen, 2006), biological motion

(Norman et al., 2004a), shape-from-motion (Norman et al., 2006), binocular rivalry (Norman et al., 2007), and motion in 3-D (Jiang, Greenwood, & Parasuraman, 1999; Norman et al., 2004b). Patients with Alzheimer's disease who have normal static visual acuity and preserve simple motion direction discrimination, exhibit deficits in perceiving shapes defined by motion cues (Gilmore et al., 1994; Rizzo & Nawrot, 1998; Rizzo et al., 2000).

Previously, we reported that older adults showed improved performance in perceiving motion signals by increasing luminance intensity and contrast in the motion displays. However, older adults could not overcome the deficits in processing successive motion signals. Specifically, we reported an age-related deficit in processing rapid motion sequences in visual priming tasks (Jiang, Greenwood, & Parasuraman, 1999; Jiang, Luo, & Parasuraman, 2002b). Perceptual priming is a form of implicit memory. Perception tends to be easier and performance tends to be more efficient upon a second repetition of a given task. Accordingly, visual priming refers to the effect that prior perception of a stimulus can bias the perception of a subsequent stimulus. For instance, first seeing a young woman's picture can bias the famous old lady/young woman bi-stable picture into being perceived as a young woman. Previous studies on priming, such as semantic and perceptual priming using static visual stimuli have been widely studied (e.g., Neely, 1991; Parasuraman & Martin, 2001; Posner & Snyder, 1975). Neural correlates of various priming effects have also been investigated using event-related potentials (ERPs), e.g., using letters (Aaltonen et al., 1992), words (Bentin, Kutas, & Hillyard, 1995; Brown, Hagoort, & Chwilla, 2000; Holcomb, 1993; Friedman, 1992; Paller & Gross, 1998; Rugg, 1987), affective words or images (Zhang et al., 2006); faces (Begleiter, Porjesz, & Wang, 1995; Olivares et al., 1994; Paller et al., 2000), pictures (Berti et al., 2000; Cycowicz & Friedman, 1999; Stelmack & Miles, 1990), motion (Jiang, Luo, & Parasuraman, 2002a) and objects (Ranganath & Paller, 2000; Lawson, Guo, & Jiang, 2007). Among the many forms of perceptual priming, visual motion priming refers to a previous motion influencing the perception of later motion events. Visual motion priming has been demonstrated for 2-D movement perception (Pinkus & Pantle, 1997; Anstis & Ramachandran, 1987) and for 3-D rotation in depth (Jiang, Pantle, & Mark, 1998; Nawrot & Blake, 1993). Presently, age-related differences in visual motion priming are not well understood.

The present study was designed to examine the underlying neural mechanisms of age-related reduction of visual motion priming reported in our previous study (Jiang, Luo, & Parasuraman, 2002b). Since motion priming is strongest when the prime-target interval is less than 400 ms, we recorded event-related potentials (ERPs), which have high-temporal resolution, in the prime-target intervals of 200 ms, 400 ms, and 1000 ms. These recordings were done in both younger and older groups while they performed a motion priming task. In two ERP experiments, we used a 2-D motion priming paradigm adapted from Pinkus and Pantle (1997) in younger and older adults. In Experiment 1 we compared younger and older neural responses to a single leftward or rightward movement (unambiguous and ambiguous conditions) (Figure 1). Then, in Experiment 2, we examined prime-target motion perception (double motion jumps) in the two age groups.

Experiment 1

We first examined ERPs to single-step moving sine-wave gratings in younger and older adults. Because older adults have lower contrast sensitivity than younger adults (Kline & Scialfa, 1996; Scialfa et al., 1992), older adults have difficulty detecting motion or motion-defined surfaces and in discriminating the direction of motion at near-threshold conditions or when contrast is poor (Andersen & Atchley, 1995; Gilmore et al., 1992; Owsley, Sekuler, & Siemsen, 1983; Trick & Silverman, 1991; Warren et al., 1991). To eliminate the possible confounding of an age-related difference in priming from age-related differences in motion perception sensitivity, we used the motion direction judgments of single motion jumps using high-contrast

stimuli well above-threshold, which has been shown to be age-equivalent in perceptual judgments (Jiang, Luo, & Parasuraman, 2002b). The aim of the first experiment was to compare the amplitude and latency (the time lag from stimulus to the peak of an ERP component) of the neural response associated with visual motion perception of single motion jumps in both younger and older adults. The single motion jumps later served as a prime-target pair in the second, motion priming, experiment.

METHODS

Participants

Seventeen younger adults, ages 18–26 (mean age 22), and thirteen older adults, ages 63–79 (mean age 72), judged the directions of motion in two experiments while EEG were recorded. The younger participants were college students from The Catholic University of America in Washington, DC. The older group consisted of community-living adults with no signs of cognitive impairment as assessed by the Mini-Mental State Examination (MMSE). The younger and older adult groups had similar educational levels. Both younger and older participants had corrected vision of at least 20/40 in Snellen and Rosenbum eye examination tests.

Visual Display and Experimental Design

The apparent motion jumps were viewed through a circular hole in a cardboard sheet 16 cm in diameter, at a viewing distance of 104 cm (8.8° of visual angle; Figure 1(A)). They were constructed as in the 2-D motion priming experiments reported by Pinkus and Pantle (1997). The average luminance of the display was 14 cd/m², Michelson contrast for each frame was 48%, and spatial frequency of the sine-wave gratings was 0.7 c/deg. The refresh rate of the computer was 75 Hz.

Each motion signal consisted of apparent motion frames: the first sine-wave pattern (0°), followed by the second frame (+/−90° or 180°). The three types of single movements were: (1) unambiguous left; (2) unambiguous right; and (3) ambiguous (left or right). A −90° phase shift in a sine-wave grating is associated with perception of an unambiguous single motion step to the left (Figure 1B). A +90° phase shift in a sine-wave grating is associated with perception of an unambiguous single motion step to the right. A 180° counterphase shift between frames results in perception of movement to either the left or right, with equal probability even though the physical stimuli remain the same (ambiguous or bistable motion) (Figure 1C). There were 80 trials of each single motion condition (unambiguous left, unambiguous right, or ambiguous). We used a 5 second inter-trial interval to avoid possible priming between two successive trials. To minimize the possibility of response biases by the participants, the three conditions were presented in a counterbalanced order.

Procedure

Participants were instructed to look globally towards the center of a computer screen. After viewing each motion jump, they reported each motion direction (right or left) by pressing the corresponding button in either their left or right hand. They were told to respond as soon as they saw the motion, and to press both buttons if they were not sure of the motion direction or if they missed seeing the stimuli because they blinked.

EEG Recording and Data Analysis

The electroencephalogram (EEG) was recorded from 14 scalp electrodes at Fz, Cz, Pz, Oz, C3, C4, P3, P4, T5, T6, O1, O2, OL, and OR, with the reference on the right mastoid. The OL and OR sites were located halfway between O1 and T5 and halfway between O2 and T6

respectively. The EEG and the two eye channels were amplified with a bandpass of 0.1–100 Hz and continuously sampled (250 Hz/channel) for off-line analysis following removal of eye movement and blink artifacts ($>\pm 75$ V). Each ERP component was measured relative to a 200 ms baseline preceding the onset of the stimuli. The averaging epoch for ERPs was 1000 ms including a 200 ms pre-stimulus baseline.

ERPs were selectively averaged to the last apparent motion frame. Peak amplitudes were determined by calculating the value from baseline to the respective peak. Results were expressed as mean $\pm$ standard error (SE). EEG epochs were averaged separately for the rightward, leftward and ambiguous motion conditions. The numbers of individual trials per ERP waveform for each condition ranged from 43 to 59 (mean 52). The following ERP components were consistently observed: P1 (50–150 ms), N1 (100–200 ms), and LPC (250–550 ms). The mean amplitudes and latencies were computed for the P1, N1, and LPC components of the ERP.

The latencies and amplitudes of ERP components were analyzed using repeated measures analyses of variance (ANOVAs) with one between-group factor: age (young or old) and two within-group factors: motion direction (leftward, rightward or ambiguous) and electrode site (four sites for the anterosuperior N1, seven sites—T5, T6, OL, OR, O1, O2, Oz—for the inferoposterior P1 and N1, and 14 sites for the LPC component). The p values of all main and interaction effects were corrected using the Greenhouse-Geisser method for repeated-measures effects. In comparing the scalp distributions of different components, the data were first normalized to control for distribution $\times$ electrode interactions resulting simply from differences in component amplitude (McCarthy & Wood, 1985).

RESULTS AND DISCUSSION

The younger and older observers performed with an equal consistency. When perceiving leftward or rightward single unambiguous motion steps, both groups achieved an accuracy rate of over 90%. When motion was ambiguous, both groups responded with similar amounts of right-left choices, both at around 50–50, chance level (cf. Pinkus & Pantle, 1997; Jiang, Luo, & Parasuraman, 2002b). In the unambiguous single motion steps, there was no age effect in the proportions of perceptual judgments of the direction (left or right). The single motion step was perceived correctly 96% of the time by the younger adults and 92.5% of the time by the older adults. In the ambiguous single motion step, younger and older adults perceived the motion at about chance level. The average proportions of individual right-left choices were 59% and 56% for the younger and older groups respectively.

For both age groups, there were no significant differences in ERP component amplitudes or latencies between the unambiguous leftward and rightward motion conditions (Figure 2). Thus, there was no difference in the neural response associated with judging the direction of unambiguous single motion jumps to the left or the right ($p > 0.10$). There was significant main effect of electrode sites for P1, N1 and LPC amplitude ($p < 0.01$), which means ERP responses varied at different scalp locations. Topographic maps revealed the P1 component showed the largest responses at occipital and posterior temporal scalp sites, whereas N1 had a wider distribution range over occipital and temporal sites. The LPC was distributed broadly over central and posterior sites. For both age groups, the mean amplitude of the LPC elicited by ambiguous motion (3.8 ± 0.34 μ V) was significantly smaller than that for unambiguous motion [5.6 ± 0.47 μ V, $F(2,56) = 32.19$, $p < 0.0001$; Figure 2]. It is noteworthy to mention here that LPC or P3 amplitude is often used as a measure of processing capacity. Interestingly, task difficulty and task engagement such as attention, have opposite effects on the amplitude of LPC (Kok, 2001). An increase in task difficulty transforms the flow of information in the processing systems and thus affects the underlying LPC generation. The reduced LPC

amplitude is likely due to the fact that perception of ambiguous motion is more difficult than that of unambiguous motion.

Age-related Effect in ERPs Latency in Judging Single Motion

The age $\times$ P1 latency interaction was significant [$F(2,56) = 10.46$; $p < 0.001$]. Between the two age groups, significant differences were also found for the latency of N1 and LPC. The N1 components of the older participants appeared to be slightly smaller, but there was no significant amplitude difference between the two age groups. As seen in Figure 2, the latency of N1 was significantly longer in older adults (175 ms) than in younger adults [145 ms, $F(1,28) = 17.13$, $p < 0.001$]. In addition, the LPC responses to ambiguous motion versus unambiguous motion were slower in the younger group (414 ms ambiguous and 374 unambiguous), but not in the older group (400 msec ambiguous and 404 msec unambiguous). This effect is similar to the P1 latency result and approached significance [$F(2,56) = 2.9$, $p = 0.063$].

The results of Experiment 1 confirmed that the patterns of ERP responses of the older group were not significantly different in amplitude compared to those of the younger group. Though the two age groups were similar behaviorally when making perceptual motion judgments, there were age-related differences in ERP response latency associated with the motion perception. Also, noticeably, the neural responses to motion direction of the older adults returned to baseline at least 200 ms later than the neural responses of the young (Figure 2).

Experiment 2

The ERP results of Experiment 1 provided temporal characteristics of the neural responses of younger and older participants to ambiguous and unambiguous *single* motion stimuli. In Experiment 2, the age effect on the neural responses to *two* successive motion stimuli was examined.

A target stimulus that is usually perceived as moving ambiguously can be disambiguated (or primed) by previous exposure to a stimulus that moves unambiguously in one direction. If the prime stimulus moves left, participants typically report the subsequent ambiguous target motion as also to the left. This priming effect is transient and typically decays to chance level over a prime-target interval of one second (Pinkus & Pantle, 1997). The current experiment used this prime-target paradigm to examine ERPs associated with motion priming in younger and older adults. ERPs were recorded in younger and older adults while they judged whether two successive motion steps were in the same (priming) or opposite (motion reversal) directions (Figure 3). In the motion priming condition, an unambiguous jump (left or right) was followed by an ambiguous jump. In the motion reversal condition, two unambiguous jumps occurred in succession but in opposite directions (e.g., left-right or right-left) and thereby provided a control condition. Perceptually, older adults report reduced motion priming compared to younger adults (Jiang, Luo, & Parasuraman, 2002b).

Visual Stimuli and Experimental Design

Both motion priming and motion reversal (control) conditions were used in the present experiment. Figure 3 illustrates the phase shifts between successive frames. In the priming condition the phase shifts were in the sequence of either 0° , -90° , $+90^\circ$ or 0° , $+90^\circ$, -90° . This resulted in an unambiguous movement to the right or left (90° shift), followed by an ambiguous movement (180° shift). In the motion reversal (control) condition the phase shifts were in the sequence of 0° , $\pm 90^\circ$, 0° , which was perceived consistently as two opposite motion directions (right then left, or left then right). This is because 90° phase shifts, whether left (0° , -90°) or right (0° , $+90^\circ$) are unambiguous.

There were three time intervals between prime and target, i.e. between the first and second motion steps: 200 ms, 400 ms, and 1000 ms. Motion priming is strongest when SOA is under 200 ms; it is reduced to weak priming at an SOA of 400 ms. Priming is close to chance level at around 1000 ms. These intervals were selected on the basis of previously established results (Pinkus & Pantle, 1997; Jiang, Greenwood, & Parasuraman, 1999). For each prime-target time delay, a motion reversal (control) condition was also used. The priming and motion reversal (control) conditions were counter-balanced. There were 80 trials in each of the six conditions.

Procedure

In the prime-target priming paradigm, participants were presented with successive pairs of motion stimuli. Younger and older adults reported whether the two motion jumps were in the same direction or in the opposite direction by pressing either the right or left button. To minimize the influence of possible response bias, half of the participants pressed the left button to indicate “same direction” and the right button to indicate “opposite directions”. In the other half of the participants the buttons were reversed.

EEG Recording and ERP Data Analysis

The EEG was recorded in the same way as Experiment 1, except Experiment 2 used a 1000 ms pre-stimulus baseline. ERPs were averaged to the last motion frame for a 1000 ms epoch and were averaged separately for each of the six combinations of motion conditions (priming or reversal) and prime-target intervals. ERP components were quantified in the same way as Experiment 1. The latencies and amplitudes of ERP components were analyzed using repeated measures ANOVAs with one between-group factor: age (younger or older) and two within-group factors: motion condition (priming or reversal) and electrode site (as in Experiment 1).

RESULTS AND DISCUSSION

Perceptual Judgment of Priming

In both age groups, strong visual motion priming occurred when the prime-target delay (SOA) was 200 ms, weak priming occurred under SOA of 400 ms, and no priming occurred under SOA of 1000 ms. Although both groups were able to clearly perceive the motion stimuli, the older adults showed reduced visual priming under SOA of 400 ms, as seen in Table 1. In the motion reversal (control) condition, older adults were just as sensitive as younger adults in detecting two successive motions in opposite directions. Although there was no significant age-related difference in perceived motion reversals, older adults did show larger individual differences in responses compared to the younger adults.

ERPs of Priming and Reversals at Three SOAs

The ERP results associated with motion priming are described separately for each of the three prime-target intervals. At a 200 ms SOA between the prime and target motion jumps, there was strong behavioral evidence of motion priming. At a 200 ms SOA (strong priming) (See Figure 4B, Top Panel), relative to the baseline reversal conditions, motion priming was associated with significantly more positive-going ERP activity at both early [posterior P1: priming: 2.21 μ V; motion reversal: 1.76 μ V; $F(1,28) = 4.16$, $p = 0.05$] and late stage LPC [priming: 5.03 μ V; motion reversal: 3.89 μ V; $F(1, 28) = 12.99$, $p = 0.001$].

When examining ERP responses at the SOA of 200 ms (strong priming), the interaction between age and posterior P1 responses to motion priming and reversals was significant, $F(1, 28) = 12.56$, $p = 0.001$. In the priming condition the P1 at the posterior temporal and occipital sites was larger in the younger group than in the older (3.0 vs. 1.42 μ V); yet, there was no significant difference between the two age groups in the motion reversal (control) condition

(1.76 vs. 1.76 μV). In both the priming and motion reversal (control) conditions the latencies of the posterior P1 and LPC were much later in the older than in the younger (Figure 4; [P1: 108 vs. 132 msec, $F(1,28) = 10.12$, $p = 0.004$]; LPC [434 vs. 477 ms, $F(1,28) = 7.27$, $p = 0.01$]).

At the 400 ms SOA (weak priming), again there was a significant interaction between P1 amplitudes and age group for both conditions [$F(1,28) = 5.37$, $p = 0.03$]. Averaged P1 response to motion priming was similar in the two age groups (P1 amplitude was 2.2 μV in younger adults and 2.25 μV in older adults). Averaged P1 response to motion reversal, however, was different (1.81 μV in younger adults and 2.60 μV in older adults). In terms of N1 amplitude, interaction between motion types and age group was also significant [$F(1,28) = 5.67$, $p = .02$]. Most strikingly, LPC response amplitude showed strong interaction with age [$F(1,28) = 23.4$, $p < .001$]. As seen in the middle waveforms of Figure 4, the younger adults evoked much larger LPC responses for motion priming ($4.88 \pm 0.39 \mu\text{V}$) than for motion reversal (control) ($2.88 \pm 0.27 \mu\text{V}$). In contrast, the older adults evoked similar LPC responses to motion priming ($3.21 \pm 0.42 \mu\text{V}$) and to motion reversal (control) ($2.94 \pm 0.36 \mu\text{V}$). The latencies of the P1, N1 and LPC under SOA of 400 ms were significantly longer in the older than in the younger age group [P1: 114 vs. 95 ms respectively, $F(1,28) = 7.54$, $p = 0.01$; N1: 201 vs 146 ms, $F(1,28) = 33.8$, $p < .001$; and LPC: 476 vs. 426 ms, $F(1,28) = 10.18$, $p = 0.003$]. The older adults' ERP response to the second motion stimuli was about 20 – 50 ms delayed compared to the younger adults.

Finally, at the SOA of 1000 ms (no priming), there were no significant amplitude differences between the ERPs for motion priming and motion reversal (control) conditions at either the early or late stages of processing following target onset. The differences between age groups occurred only in ERP latency. For the older vs younger groups respectively the latencies were: posterior P1 [123 vs 105 ms, $F(1,28) = 7.22$, $p = 0.01$] and anterior N1 [186 vs 144 ms, $F(1,28) = 25.0$, $p < 0.001$]. Similar to the single motion perception (Figure 4, Bottom waveforms), the LPC response was slower in the older (467 ms) than in the younger adults (385 ms) [$F(1,28) = 42.1$, $p < 0.001$].

ERP Difference Waves: Early Age-effect in Occipital Sites

We further examined the differences between ERPs of priming and motion reversals. The ERP difference was reduced in the older adults compared to the younger adults when the SOA is below 400 ms (Figure 4). The waveforms at midline sites Oz, Pz and Cz revealed ERP characteristics specifically associated with motion priming in the two age groups at 200 ms SOA (strong priming). P1 amplitude and latency differences were largest at the central occipital site (Oz, $p < 0.0001$). For both the younger and older groups, these priming and reversal differences were seen most strongly at Oz. We infer that the age-related changes occur as early as occipital sites. When motion priming was relatively weak (at the 400 ms interval), the P1 was maximal for the younger group at central occipital and two temporal sites, whereas the P1 was maximal for the older group at two lateral occipital regions.

GENERAL DISCUSSION

The current experiment examined electrophysiological correlates of the age effect in visual motion priming. In both age groups prior motion perception biased the subsequent perceived motion when the stimuli were presented closely in time, within 400 ms, in both age groups. However, the degree of motion priming was significantly reduced in older adults compared to younger adults. We first examined ERP responses to single ambiguous and unambiguous motion jumps. The ERP results from Experiment 1 showed that although the latencies of ERP components (P1, N1 and LPC) in the older group were significantly longer than those of the younger group, ERP amplitudes and perceptual judgments for single motion jumps were comparable both age groups. In the Experiment 2, two motion jumps were placed at three SOAs (200, 400, and 1000 ms). The perceived direction of motion of a target stimulus that moved

ambiguously to the left or the right was disambiguated by an immediately preceding prime that moved consistently in only one direction under SOA of 400 ms. However, older adults showed significantly reduced motion priming (up to 20%) compared to younger adults. Additionally, under the motion priming condition, the younger adults evoked larger ERP responses and had shorter latencies for the subsequent motion signal compared to those of the older adults.

Age-related Difference in ERPs

In the motion priming task, the ERPs were delayed in older adults (20–80 ms). The LPC latency has been shown to increase with age (see Polich, 1996). In the present experiment, the latency of P1 and N1 components (typically generated at the early visual occipital sites) were longer in the older adults, which demonstrated that the age-related changes in motion priming probably occur at a relatively early stage of visual processing (See Figure 5). Although age-related variation for the P1 and N1 components has seldom been examined in visual processing, recent studies have shown similar temporal delays in older adults in auditory tasks. For example, Federmeier et al. (2003) found similar delays of around 25 ms for N1 responses to auditory stimuli in older listeners while later components (N400) were not delayed. In the present study, LPC was also delayed in the older adults, which might be an induced delay resulting from the delay of the early P1 and N1. Additionally, Tremblay, Piskosz, & Souza (2002) reported similar age-related delays in the N1 component in response to the temporal characteristics of auditory stimuli. The first positive ERP response, i.e. the P1 component, and the LPC are considered to be modulated by spatial attention (Heinze et al., 1994; for a review see Mangun, 1995) and by color and motion (Anllo-Vento & Hillyard, 1996). In this study ERP responses tended to decrease in the older group (P1 and LPC) at the 200 ms SOA. P1 amplitude for the priming was reduced in the older group. Our results suggest that age-related deficits in visual processing or attention occur in early visual processing around 100 ms.

A Psychophysics Model—A previous psychophysics study has applied a “motion energy” model to explain the visual motion priming effect (Pinkus & Pantle, 1997). The perceptual decision of unambiguous motion direction was decided by a majority of directional neurons favoring one direction (left or right). In the case of ambiguous motion, equal leftward and rightward motion energy led to left or right perceptual decisions at the 50–50 chance level. When placed close in time, the neural response to unambiguous motion influences the response to subsequent ambiguous motion in the direction that possesses more residual motion energy. By applying this model to our study, one could propose that in younger adults the neural response to unambiguous prime motion has more power or motion energy to bias the ambiguous target motion than in older adults.

When the SOA was 400 ms, the younger adults showed about 80% visual motion priming while the older adults perceived on average about 60% of priming (i.e. the second perceived motion was in the same direction as the first motion about 60% of the time). In the younger group, significantly larger ERPs were evoked by the motion priming condition than by the motion reversal (control) condition. In the older group, however, differences in ERP responses between priming and reversal were reduced. At the longest SOA (1000 ms) neither ERP amplitude differences between conditions nor perceptual priming effects occurred in either age group. In other words, when two motion signals are far apart (1000 ms), there was no age difference in ERP response strength. The age-related deficit is in processing successive motion signals.

Age-related Changes in Neural Responses

Our ERP results on perceptual priming revealed that the age-related reduction in perceiving visual motion may be due to the delayed ERP responses of older adults. This may not affect perceptual decisions for a single motion step, but when two motion stimuli occur closely in-

time, the older brain becomes more vulnerable to perceptual indecision. In other words, the motion energy associated with the initial stimulus is weaker for older brains and less able to influence the direction of the perceived target motion. In turn, the perceived motion occurs at more of a chance level rather than being biased by the prior perception. Accordingly, our results showed that under an SOA of 400 ms, older adults had diminished differences between the ERP responses to motion priming and motion reversal.

Our results which indicate reduced motion priming point to age-related changes in temporal characteristics of cortical responses to visual motion. These changes make older adults more vulnerable when processing successive motion stimuli. Interestingly, such brain aging changes sometimes improve the perception of motion. For example, Betts et al. (2005) report that aging alters center-surround interactions in ways that improve performance in discriminating the direction of motion. They argue that older observers required briefer stimulus durations than did younger observers to extract information about stimulus direction in conditions using large, high-contrast patterns. They suggest that this is due to weaker center-surround antagonism in senescence, perhaps attributable to age-related reduction in inhibition in motion-selective neurons. In the case of motion priming, if older adults require shorter durations for processing direction information, the prime motion would have a smaller impact on the second perceived motion, compared to the priming effect of the younger adults. Reduced priming might be the result of the second motion signal being perceived more independently in the older observers.

Age-related Changes in Network of Visual Cortices

Older adults may have deficits in parts of cortical regions responsible for disambiguating motion directions. Recent evidence from magnetoencephalography (MEG) demonstrated that visual perception of 2D shape-from-motion elicits sequential activity of a network of cortical regions (Schoenfeld et al., 2003). Visual perception of 3D shape-from-motion elicits activity in occipital (~100 ms), temporal (~200 ms) and parietal (~300 ms) cortices in the human brain within 400 ms. At about 500 ms, long lasting activity was observed in the parietal cortex and concurrently in previously activated regions (Jiang et al., 2008). Using single-cell recordings, Williams et al. (2003) reported an interesting finding at several areas of monkey brains. Their findings revealed that unambiguous motion (our prime stimuli) activated the motion perception area (MT/MST) but ambiguous motion (our target stimuli) showed little MT activity but activated neurons in the lateral intraparietal area (LIP). This supports the view that ambiguous motion is processed in the parietal lobes in humans (Leopold, 2003). Using functional magnetic resonance imaging (fMRI) techniques, Jiang, Luo, & Parasuraman (2002a) reported that occipital, middle temporal (MT), superior temporal sulcus, and parietal areas in the visual cortices were involved in the motion priming task.

Figure 5 illustrates that brain aging alters cortical processing to disambiguate motion directions in a network of visual cortices. The current results for P1 showed age-related differences occur as early as 100 ms in the early visual cortex, which indicate possible age-related changes in visual attention. The amplitude of LPC (P3 or P300) is influenced by many cognitive factors such as attention, recognition, confidence, content updating and task difficulty (Kok, 2001). LPC is generated from central parietal cortices (e.g. Dien, Spencer, & Donchin, 2003). If the parietal lobes in humans are responsible for resolving motion ambiguity and perceptual decision ambiguous motion processing, future studies using multi-modal imaging should test the hypothesis that occipital-temporal-parietal circuits are more vulnerable to brain aging.

In summary, the present study provides electrophysiological evidence that brain aging changes the characteristics of cortical responses to motion stimuli as early as 100 ms in the early visual cortex. Additionally, age-related changes in strength and temporal characteristics of neural responses were particularly pronounced in the temporal-parietal network of older adults when successive motion signals are placed closely in time within 400 ms.

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Figure 1.

Experiment 1: (A) Visual stimuli for single apparent motion from sine wave gratings. (B) The 90° phase shift results in perception of a single motion step to the left. (C) The 0° – 180° counter-phase shift between frames results in perception of movement to either the left or right (ambiguous or bistable).

Figure 2. Grand-average ($n = 17$ for young and $n = 13$ for older adults) ERP waveform and topography of the N1, P1, and LPC components for leftward, rightward and ambiguous single motion jump.

Double motion steps **Figure 3.**

For each of the three SOAs (200, 400 and 1000 ms) between first and second motion steps, there were two types of motion stimuli: motion priming (left panel; perception of left-left or right-right motion) and motion reversal conditions (right panel: perception of right-left or left-right motion).

Figure 4.

Grand-average ERPs of the motion priming and reversals waveforms at midline sites Cz, Pz and Oz. For both the younger and older groups, motion priming is strongest for the 200 ms SOA, weaker for the 400 ms SOA, and insignificant for the 1000 ms SOA.

Figure 5.

Proposed visual processing stages and cortical network involved in visual motion priming, based on current and previous results. The right panel summarizes the timing of ERP responses in younger and older brains. The left panel summarizes the role of each stage of the cortical network. The early visual cortex in the occipital area processes luminance, contrast and directions of visual stimuli (P1/N1, about 100 msec). The MT/V5, visual motion processing area, processes unambiguous motion directions, and the parietal regions make perceptual decisions influenced by motion priming.

Table 1

The percentage of perceived motion directions in the same direction (% priming)

	SOA (ms)	Young (n=12)	Old (n=12)
Motion Priming	200	93±1.7	81±2.4
	400	83±1.8	63±3.4
	1000	55±2.5	39±3.4
Motion Reversal	200	6±1.5	12±4.0
	400	6±1.5	14±4.7
	1000	8±1.7	17±4.7

(Notes: Mean % ± SE; see discussion in Jiang, Luo, & Parasuraman, 2002b)