

Qing. Yang · Zoï. Kapoula

The control of vertical saccades in aged subjects

Received: 18 May 2005 / Accepted: 11 October 2005 / Published online: 24 November 2005
© Springer-Verlag 2005

Abstract In real life we produce vertical saccades at different distances and eccentricities, and while our fixation is more or less actively engaged. The goal of this study is to examine vertical saccades in aged and young subjects, taking into consideration all these parameters. Eleven adults (20–28 years) and 11 aged subjects (63–83 years) were recruited. We used LED targets at 7.5° or 15°, up or down in four conditions: gap and overlap tasks, each done at two distances—at near (40 cm) and at far (150 cm). In the gap task fixation target extinguishes prior to target onset, while in the overlap condition it stays on after target onset; consequently, visual attention and fixation are employed differently in the two tasks. Eye movements were recorded with the Chronos video eye tracker. Results showed that vertical saccades were longer for aged subjects than for young adults under almost all conditions. For both aged and young subjects, latencies were shorter under the gap than under the overlap task. Latencies for eccentric targets at 15° were significantly longer than those at 7.5° but for aged subjects only; this effect was more pronounced for upward saccades under the overlap condition. Express type of latencies (80–120 ms) occurred frequently in the gap task and at similar rates for young adults (16%) and aged subjects (12%); in the overlap task express latencies were scarce in young adults (0.4%)

and aged subjects (1.8%). Age deteriorates the ability to trigger regular volitional saccades but not the ability to produce express type of saccades. Latency increase with aging is attributed to the degeneration of central areas, e.g. oculomotor cortical areas involved in the initiation of vertical saccades.

Keywords Aging · Vertical saccades · Gap–overlap · Volitional control · Cortical degeneration · Express latencies

Introduction

Latency of saccades is increased when the initial fixation point remains illuminated during the appearance of the new target (overlap task) and is reduced when the initial fixation point disappears some time prior to target onset (gap task). This difference in the latency between the gap and overlap conditions is termed the gap effect (Saslow 1967; Fischer and Weber 1993; Munoz and Corneil 1995; Pratt et al. 1997; Munoz et al. 1998; Coubard et al. 2004). Such gap effect exists for horizontal saccades over all ages until 88 years old (Fischer et al. 1997a; Munoz et al. 1998; Klein et al. 2000a), and for vertical saccades in normal young adults (Goldring and Fischer 1997). In addition to the overall reduction of saccade latency in the gap paradigm, a distinct population of ultra short latencies—the so-called express saccades—appears with latencies ranging between 80 and 120 ms (Fischer et al. 1997b; Gezeck et al. 1997). However, little to nothing is known about the existence of a gap effect, and of express latencies for vertical saccades in aged subjects.

The physiological significance of gap and overlap tasks is now established. The gap task provokes rapid initiation of eye movements due to disengagement of oculomotor fixation (Ross and Ross 1980, 1981; Reuter-Lorenz et al. 1991; Kingstone and Klein 1993). In contrast, the overlap task requires volitional control to disengage fixation and/or attention from the fixation point to direct them towards the new target. At the

Grant/financial support: European Union (QLK6-CT-2002-00151: EUROKINESIS) and CNRS/CTI, Handicap contract CR:N.

Q. Yang (✉) · Z. Kapoula
Laboratoire de Physiologie de la Perception et de l'Action,
UMR 7152, CNRS - Collège de France, 11, place Marcelin
Berthelot, 75005 Paris, France
E-mail: qing.yang@college-de-france.fr
Tel.: +331-44-271636
Fax: +331-44-271382

Q. Yang
Laboratory of Neurobiology of Shanghai Institute of Physiology,
Institutes of Biological Sciences and Laboratory of Visual
Information Processing of Biophysics Institute, Chinese Academy
of Sciences, 200031 Shanghai, China

cortical level it is known that the gap paradigm activates a posterior network, and is believed that express type of latencies involve activation of retino-occipital-parietal-superior colliculus circuit while the overlap paradigm involves activation of a more extended circuit including the frontal lobe (Pierrot-Deseilligny et al. 1995, 2002). For example, Schiller et al. (1987) found an increase in the number of saccades falling into the express range after unilateral lesion or ablation of superior colliculus but not after the ablation of frontal eye field. Thus, the use of these two paradigms in aged subjects is of major interest in allowing the exploration of cortical functioning underlying reflex-like versus voluntary oculomotor behavior.

Another interesting topic is the existence of a latency asymmetry for upward versus downward saccades, i.e., shorter latency for upward saccades than for downward saccades. Such asymmetry has been reported in monkeys (Zhou and King 2002) and in humans (Honda and Findlay 1992; Goldring and Fischer 1997). Moreover, the asymmetry was influenced by the saccade paradigm. For example, the up/down asymmetry of latency found for saccades directed to the targets was greatly reduced for the antisaccades (saccades opposite to the targets) and this under both gap and overlap conditions (Honda and Findlay 1992; Goldring and Fischer 1997). In monkeys, Zhou and King (2002) reported that the latency asymmetry of vertical saccades was almost abolished in the overlap condition. Recently, similar results have been reported in humans by our group (Tzelepi et al. 2005). Thus, the asymmetry seems to be more frequent for the gap paradigm. The other important aspect we want to emphasize here is that there are big idiosyncratic differences in up/down asymmetry even in the gap condition. Miller (1969) found no asymmetry in their study, and in the studies of Honda and Findlay (1992), and of Goldring and Fischer (1997) 9/13 and 9/12 subjects respectively showed shorter latencies for upward saccades. Whether up/down asymmetry exists in aged subjects is not known.

Prior studies of horizontal saccades from our group (Yang et al. 2002; Bucci et al. 2004) revealed an effect of proximity on the latency of horizontal saccades: latency was shorter at near (20 cm) than at far (150 cm) viewing distance. This is attributed to the facility in disengagement of attention and/or of oculomotor fixation. It should be noted that in everyday life we make saccades at different distances, directions and eccentricities, and under different conditions, i.e., while concentrated on a task or being at the state of inattention or released. The goal of this study is to create a more comprehensive pool of data describing the influence of aging on the latency of vertical saccades, and also the role of oculomotor task (gap and overlap), of direction (upward and downward), of eccentricity (amplitude at 7.5 and 15°), of viewing distance (close and far), and the possible interaction among these factors. To our knowledge, such complete study of vertical saccade latency has never been made in adults and particularly in elderly.

Methods

Subjects

Eleven subjects aged between 63 and 83 years (mean age 70 ± 8) and eleven young adults, 20–28 years (mean 23 ± 2 , female eight and male three) participated in the study. All aged subjects were female and their prior professional activity was classic dance in the Governor Opera in Paris. All of them maintained sport and artistic activity, and were in perfect physical and intellectual form. The reason for such recruitment was to exclude any latent pathology and to assess the effect of aging itself.

All young subjects were students from the laboratory and had normal or corrected visual acuity. Aged subjects had corrected visual acuity more than 5/10, i.e. normal for their age. For both groups binocular vision was assessed with the TNO test of stereo acuity; all individual scores were normal, 60'' of arc or better. No subject showed visual, neurological, psychiatric disorders or received medication. The investigation adhered to the tenets of the declaration of Helsinki and was approved by the Institutional human experimentation committee. Informed consent was obtained from all subjects after the nature of the procedure had been explained.

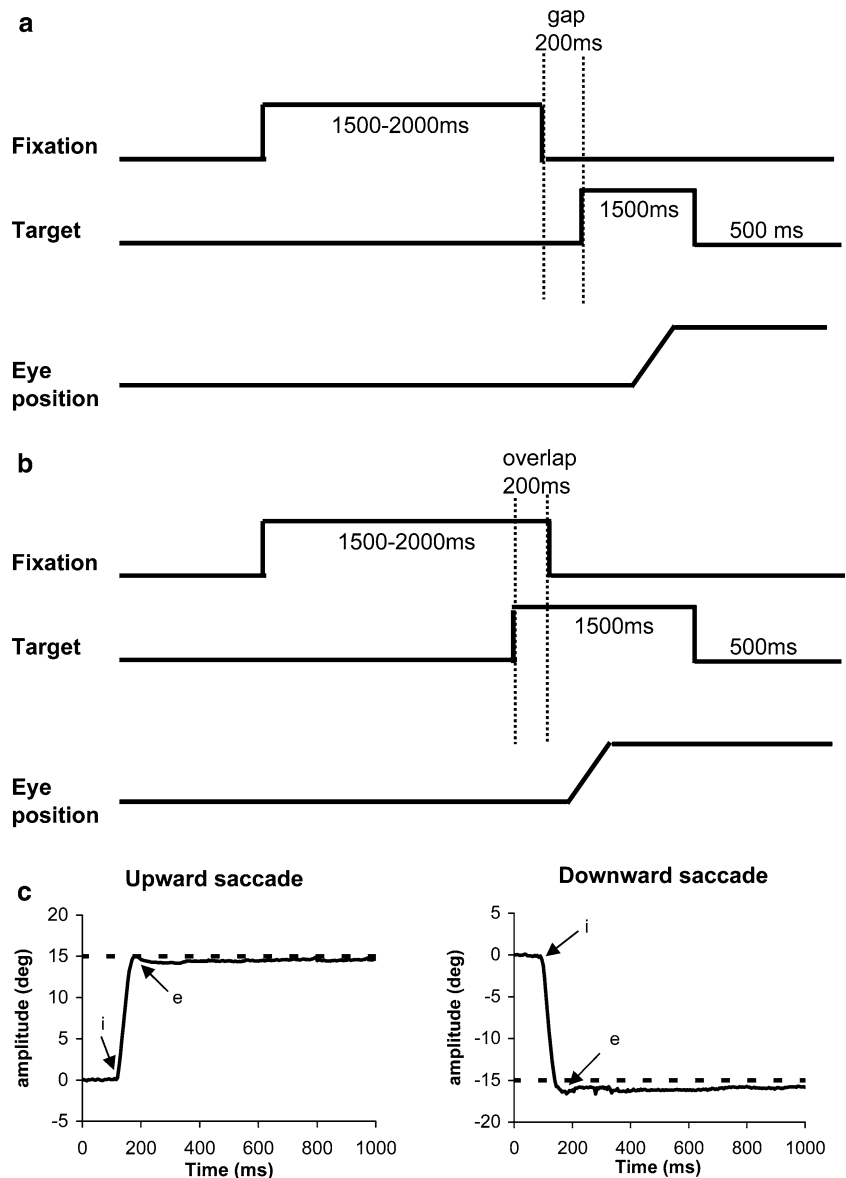
Visual display

The visual display consisted of LEDs placed on a vertical table placed at a distance of 40 cm or 150 cm from the subject's eyes. Five LEDs were used: one at the center (fixation point) and the others at $\pm 7.5^\circ$ and $\pm 15^\circ$ (up and down). In a dimly illuminated room, the subject was seated in an adapted chair with a chin and frontal rest. He/she viewed binocularly and faced the visual display of the LEDs. The center of the visual display of the LEDs was placed at eye level.

Oculomotor tasks: gap and overlap conditions

Each trial started by illuminating a fixation LED at the center. The fixation LED stayed on for a random period between 1.5 and 2 s. In the gap task, there was a time interval of 200 ms between the offset of the fixation point and the onset of the saccade target. The target LED was kept on for 1.5 s (Fig. 1a). In the overlap task, the fixation point remained illuminated for 200 ms after the target LED appeared. The target stayed on also for another 1.5 s (Fig. 1b). A period of 200 ms for both gap and overlap has been used by many other studies (Zhou and King 2002; Bucci et al. 2005); for the gap such period provided the best effects (Weber and Fischer 1995); while 200-ms overlap period is sufficient to lengthen the latency significantly (Zhou and King 2002;

Fig. 1 The paradigm used for the gap condition (a): the central fixation point disappears 200 ms before the appearance of the eccentric target; for the overlap condition (b): the central fixation point remains illuminated when an eccentric target appears. c Typical recordings of vertical saccades are obtained by averaging the position signal of the two eyes $(LE + RE)/2$. The arrows at 'i' and at 'e' indicate the onset and the end of the saccades, respectively



Bucci et al. 2005). Subjects were required to make a vertical saccade to the target LED as rapidly and accurately as possible. A blank period of 500 ms separated the trials. Subjects were instructed to use this period for blinks. The total mean length of each trial was about 4 s. In each block targets at $\pm 7.5^\circ$ and $\pm 15^\circ$ were interleaved randomly at equal rates. Each block contained 60 trials, 15 trials per target location and lasted 4 min. All subjects performed four blocks, under gap and overlap conditions at close (40 cm), and at far (150 cm) viewing distance. The order of blocks was counter-balanced for different subjects.

A calibration sequence was performed at the beginning and at the end of each block; the target made the following predictive sequence: center, 7.5° up, center, 15° up, center, 7.5° down, center, 15° down, center; the target stayed at each location for 2 s. From this recording we extracted calibration factors.

Eye movement recording

Vertical eye movements were recorded with the Chronos rapid video eye tracker which is based on high-frame rate CMOS sensors (Clarke et al. 2002). This system has an optimal resolution less than 0.1° for vertical eye movements. The sample rate was set at 200 Hz and the relevant image data (i.e. during each trial) was stored on the hard disk for offline analysis.

Data analysis

From the two individual calibrated eye position signals, we derived the conjugate signal $[(\text{left eye} + \text{right eye})/2]$. The onset of the saccade was defined as the time when conjugate eye velocity exceeded $30^\circ/\text{s}$, the offset when eye velocity dropped below $10^\circ/\text{s}$. The process was

performed automatically by the computer, and the verification was made by visual inspection of the individual eye position and velocity trace (Fig. 1c). For both gap and overlap tasks, latency was measured as the time between stimulus onset and initiation of the saccade; to evaluate the accuracy we measured the gain, e.g., the ratio movement amplitude/target amplitude. Gain data are presented briefly in the Discussion.

Eye movements in the wrong direction, with latency shorter than 80 ms (anticipation) or longer than 800 ms, or contaminated by blinks were rejected. For adults 6% of trials and for aged subjects 8% of trials had to be rejected using these criteria. We also evaluated the percentage of saccades with express type of short latency (80–120 ms) and the distribution of latencies was examined for some subjects.

Multiple factor analysis of variance (ANOVA) was performed on individual mean latencies with main factors, namely the age (young, old), the oculomotor task (gap, overlap), the viewing distance (40 cm, 150 cm), the eccentricity (7.5°, 15°) and the direction (upward, downward). Post-hoc comparisons were done with the least significant differences test. For the percentages of express saccades, the Wilcoxon test was used for within-subjects' comparisons between gap and overlap

tasks; the Mann–Whitney U test was used for comparisons between young and aged subjects.

Results

Factors influencing latency

The individual mean latencies of vertical saccades and the standard error (SE) are shown for the gap and the overlap conditions in Figs. 2 and 3. Figure 2 contains the results for the near viewing distance (at 40 cm) and Fig. 3 for the far (at 150 cm). The group means are shown at the right of each panel. All subjects showed shorter latency in the gap than in the overlap condition, except aged subject 6 (73 years) for downward saccades of 15° at the near viewing distance (Fig. 2, see arrow); aged subject 4 (66 years) and 5 (67 years) for downward saccades of 15° and of 7.5° at the far, respectively (Fig. 3, see arrows).

The multiple factor ANOVA showed statistically significant effects of age ($F_{1,20} = 8.96$, $P < 0.01$) and the gap ($F_{1,20} = 184.51$, $P < 0.0001$). The multiple factor ANOVA also revealed a significant main effect of the eccentricity ($F_{1,20} = 27.72$, $P < 0.0001$), but no statistically significant

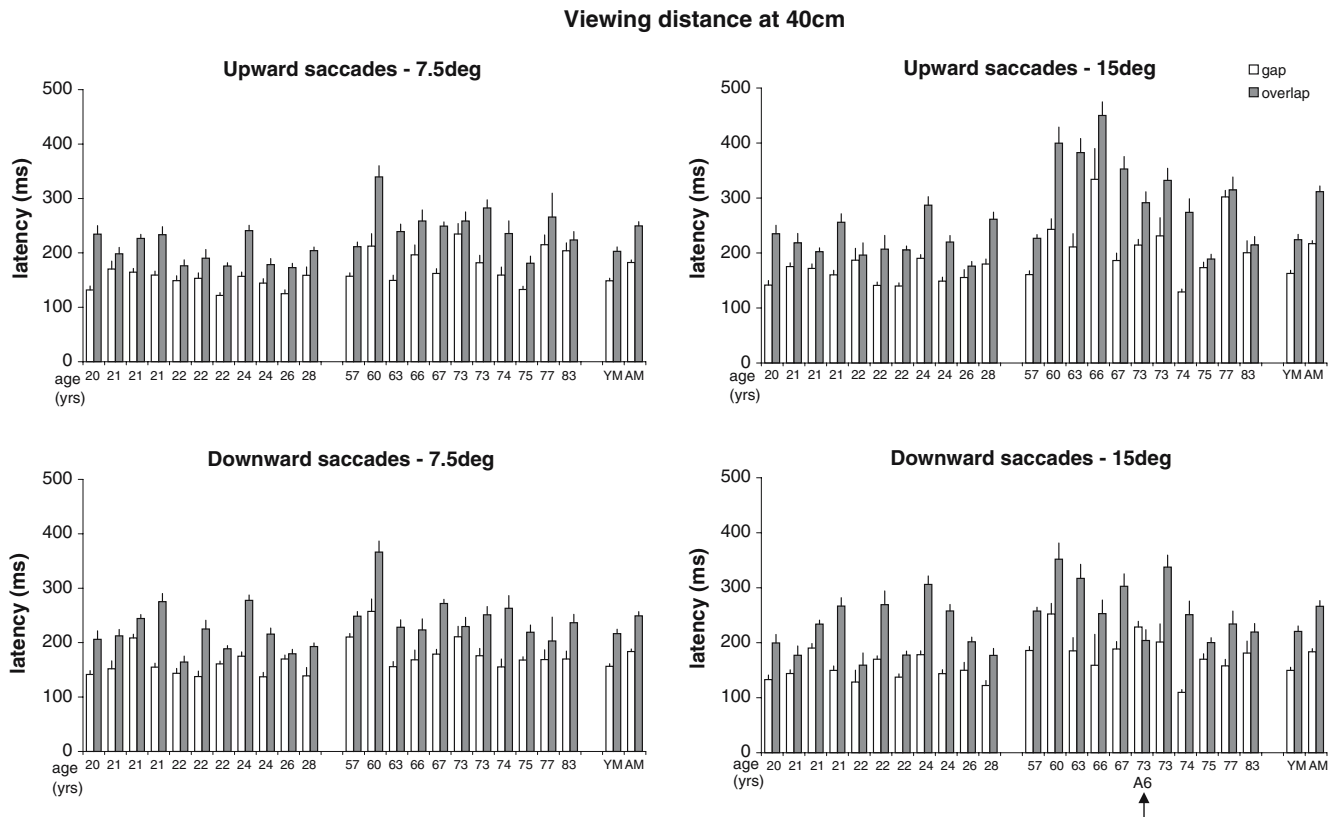


Fig. 2 Individual and group mean latency with standard errors for vertical saccades between gap and overlap conditions for both young and aged subjects at 40 cm of the viewing distance for upward saccades 7.5°, for upward saccades 15°, for downward saccades 7.5°, for downward saccades 15°

Viewing distance at 150cm

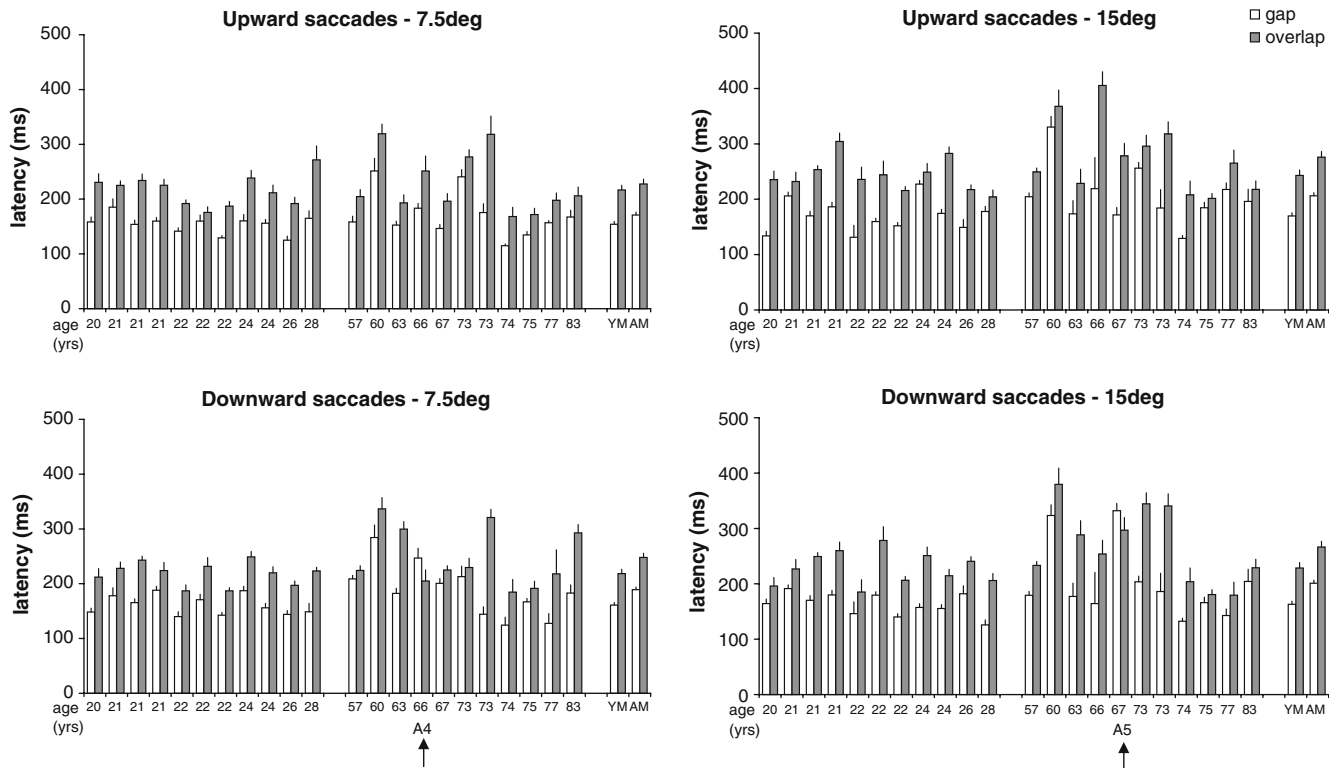


Fig. 3 Individual and group mean latency with standard errors for vertical saccades between gap and overlap conditions for both young and aged subjects at 150 cm of the viewing distance for

upward saccades 7.5°, for upward saccades 15°, for downward saccades 7.5°, for downward saccades 15°

effect of the viewing distance ($F_{1,20} = 0.05$, $P = 0.82$) and direction ($F_{1,20} = 0.44$, $P = 0.51$). The effect of the age is summarized in Fig. 4a and is of the order of 33 ms. The effect of the gap is of the order of 70 ms (see Fig. 4b). The effect of the eccentricity is small, of the order of 21 ms (see Fig. 4c).

A significant interaction was found between the eccentricity and the age ($F_{1,20} = 5.48$, $P < 0.05$, Fig. 5a); the eccentricity effect was significant for the aged subjects only, who showed longer latencies by 29 ms for target at 15° than at 7.5°, while for young subjects the difference was only 11 ms. A significant interaction was also shown between the eccentricity and the task (gap/overlap, $F_{1,20} = 5.35$, $P < 0.05$, see Fig. 5b), the latency prolongation with target eccentricity is higher for the overlap condition (26 ms) than for the gap condition (11 ms). Another significant interaction was between eccentricity and direction ($F_{1,20} = 12.78$, $P < 0.01$, see Fig. 5c); the latency prolongation with target eccentricity is higher for upward (30 ms) than for downward targets (7 ms).

In summary, the results show longer latencies in aged subjects, longer latencies in the overlap condition for both age groups, and some local effects particularly for aged subjects only, e.g., longer latencies for the most eccentric targets, particularly upward targets under overlap condition.

Express type of latencies

Figure 6 shows the percentages of express type of latencies in the gap and overlap conditions; as there was no significant difference between far and near distance, and up and down, data are regrouped for both distances and both directions. The results are shown for each eccentricity and each condition. In the gap condition all young subjects and 10 of the 11 aged subjects produced a substantial number of express latencies. The mean percentages were 17 and 15% for 7.5 and 15° for young subjects; for the aged subjects the mean percentages were 14 and 10% for 7.5 and 15° target eccentricities. The Mann–Whitney U test showed no significant difference of the percentage of express saccades between the young and the aged groups under both tasks (all $P > 0.05$). The Wilcoxon test showed significantly higher percentage of express saccades at 7.5° than at 15° ($Z = 2.1$, $P < 0.05$) for the aged subjects but no such difference for the young adults ($Z = 0.71$, $P = 0.48$).

Under overlap condition, express latency was rare; only one young adult produced express latencies (4%), and seven of the aged subjects made express type of latencies but at low rates (2–5%). The Wilcoxon test showed significantly smaller percentage of express saccades under the overlap than under gap task for both the

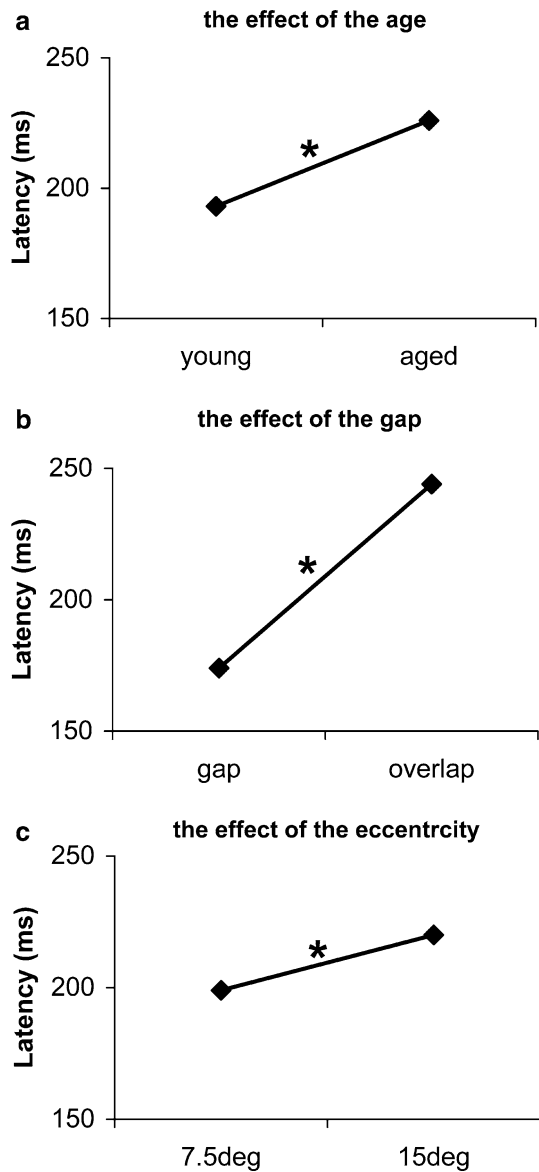


Fig. 4 Significant main effects of the age (a), of the gap (b) and of the eccentricity (c) for the latency of vertical saccades; asterisks indicate a statistically significant difference ($P < 0.05$)

young group ($Z = 2.93$, $P < 0.05$ at 7.5° or at 15°) and the aged group ($Z = 2.8$, $P < 0.05$ at 7.5° or at 15°).

We selected four young adults and four aged subjects with the higher percentages of express type of saccades to examine the latency distribution (see Fig. 7). The two vertical lines in Fig. 7 indicate the zone of express type of latencies (80–120 ms). Although such latencies were frequent for these subjects, there was no evidence for a distinct separate mode of express type. Rather, such short latencies seemed to be part of the main distribution; a later peak occurred particularly for the aged subjects. For young adults one and five, aged subject 7, only one peak of short latency was observed at 120/140 ms; for young adults 2 and 11, aged subjects 5 and 6, there were two peaks: one at 120/140 ms and the other at 180/220 ms, respectively; for aged subject 9, two

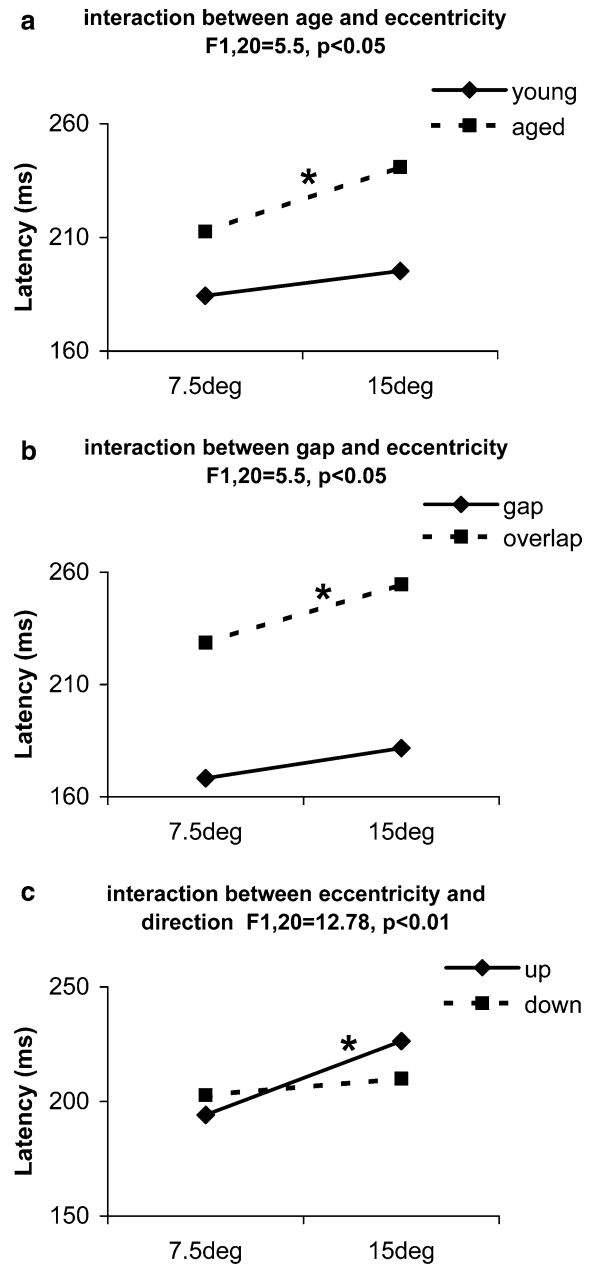


Fig. 5 The significant interaction between eccentricity and age (a), between eccentricity and task (gap/overlap, b) and between eccentricity and direction (c), asterisks indicate a statistically significant difference ($P < 0.05$)

peaks were present: one at 160 ms and the other at 200 ms.

Discussion

The main findings are as follows: latencies of vertical saccades are longer for the aged subjects than for the young adults under almost all conditions. For both the aged and the young subjects, latencies are shorter under the gap than under the overlap condition. Latencies for eccentric targets at 15° are longer than those at 7.5° .

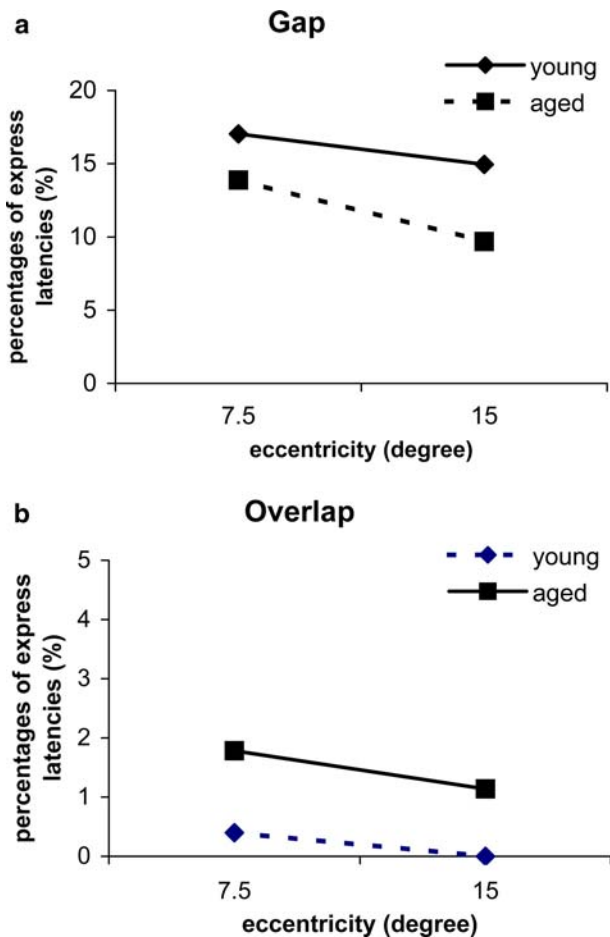


Fig. 6 Percentages of express latencies for 7.5 and 15° target eccentricities in the gap and the overlap conditions for both young and aged subjects

Such eccentricity effect is significant for aged subjects only; it is more pronounced for upward saccades under the overlap condition. The percentage of express type of saccades is higher under the gap than under the overlap condition for both groups, and there is no significant difference of the percentages of express saccades between the aged and the young subjects. Next we will discuss in more detail each of these findings.

Latency increase with aging

Studies of age differences in saccadic eye movements have focused upon horizontal saccades. Prior studies reported that horizontal saccades of the aged subjects have longer latencies than those of young subjects (Abel et al. 1983; Carter et al. 1983; Munoz et al. 1998; Klein et al. 2000b; Yang et al. 2005). Huaman and Sharpe (1993) studied vertical saccades to predictable targets and reported that aged subjects produced longer latency relative to young adults. The effects of aging we report here extend these observations for unpredictable targets in gap and overlap conditions. It is noteworthy that the

latency difference occurred in the absence of a difference in the accuracy of saccades between old and young subjects. Indeed, the mean gain was 1.002 ± 0.09 and 1.008 ± 0.07 for young subjects, in gap and overlap conditions respectively, and 0.984 ± 0.07 and 0.982 ± 0.08 for old subjects. The ANOVA run on the gain values showed no significant effect, neither of the condition ($F_{1,20} = 0.03$, $P = 0.86$), nor of the age ($F_{1,20} = 0.81$, $P = 0.38$). Thus older subjects can still produce accurate vertical saccades but with longer preparation time. Note that there was no significant correlation between latency and accuracy of the saccades neither for young nor for old subjects (both $R < 0.20$, $P > 0.05$).

During normal aging, there is widely spread atrophy of both gray and white matter in the cerebral cortex (Creasey and Rapoport 1985). Both the frontal lobe and the posterior cortex were found to undergo progressively degenerative changes with aging in humans; this was studied by means of magnetic resonance imaging (MRI) (Salat et al. 2001; Head et al. 2004). Latencies of horizontal saccades for subjects with lesions of frontal eye field increased in the overlap task (but not in gap task), and that of correct antisaccades (Rivaud et al. 1994). Voluntary saccades rely on an intact frontal system (Guitton et al. 1985), whereas reflexive saccades can be generated by the occipital–tectal system (Schiller et al. 1987). Our results in elderly showing longer latencies for regular latency but not for express saccades suggest that age effect concerns more the circuit involved for the initiation of regular saccades. The increase with senescence in mean latencies for vertical saccades may be the result of neuronal degeneration or hypofunction of one or more cerebral areas involved in the control of these eye movements. Yet, one could object that longer latencies are simply due to visual deficits, e.g., poor target localization, and/or muscular problems. In our study muscular restrictions were excluded via prior clinical examination (duction test). Corrected visual acuity of the subjects was also normal and importantly the red bright LED targets we used during our oculomotor tasks were highly visible; indeed, recordings were done in a dark experimental room requiring minimal visual acuity (1/10) to localize the LEDs. The quality of the accuracy of the saccades (mentioned above) confirms that targets were well localized by all subjects. In addition to possible cerebral hypofunction, the long latency could also be related to the degeneration of sub-cortical circuitry, such as superior colliculus (SC) and brainstem saccade generator. Thus, the increased latencies observed in aged subjects are most likely due to the delays in the cortical processing and subcortical–brainstem, e.g. shift of visual attention, sensori-motor transformation and decision and triggering mechanisms. This is further corroborated by the fact that older subjects differ from young subjects more in the overlap than in the gap condition.

Finally, one could consider an opposite view according to which longer latency indicates better voluntary control. Such view is based on observations of

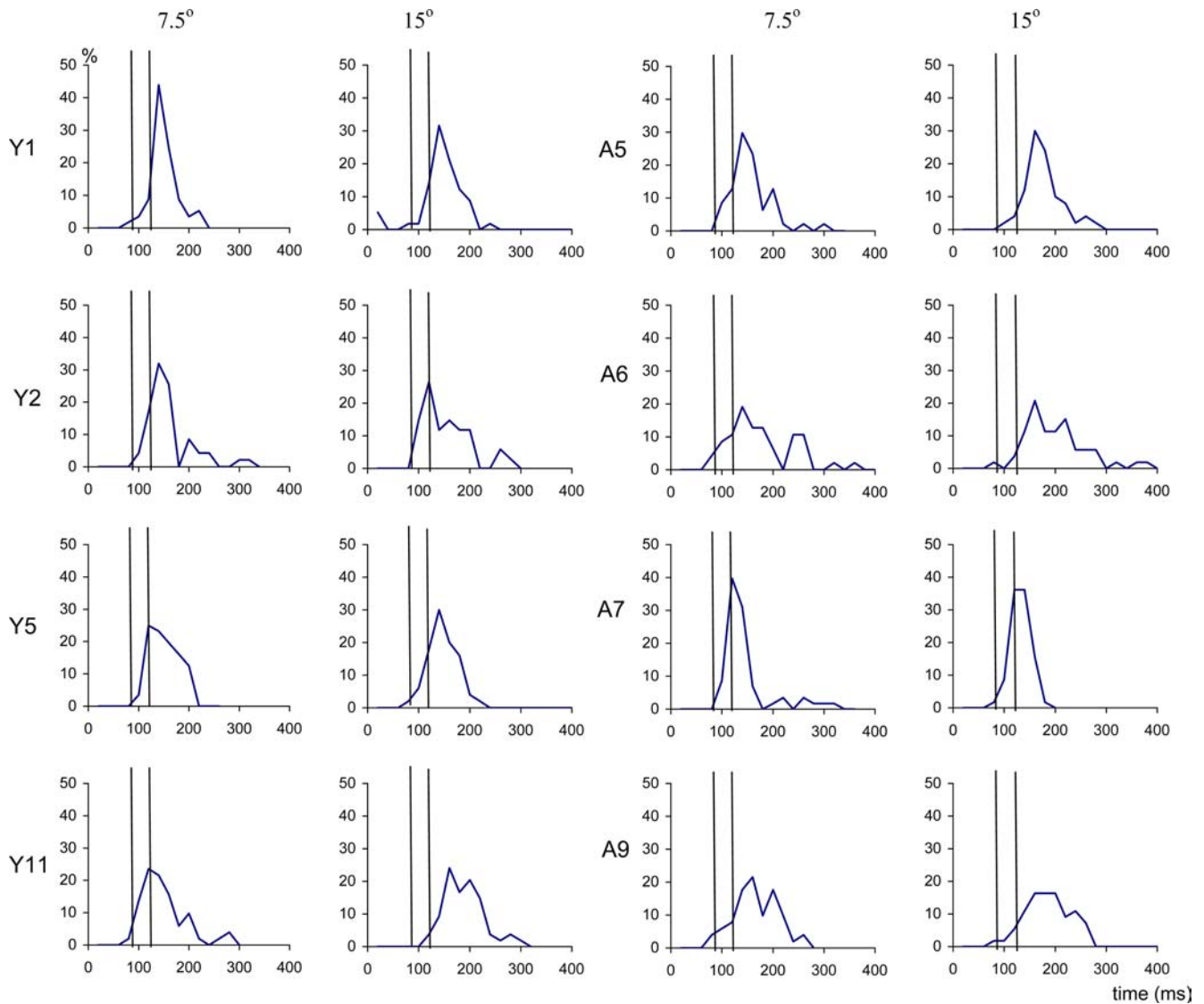


Fig. 7 The latencies distribution for young subjects (Y1,2,5,11) and aged subjects (A5,6,7,9); the two vertical lines indicate the zone of express type of latencies (80–120 ms)

abnormal short latencies and higher rates of express latencies in subjects with dyslexia or Parkinson's disease; these phenomena are attributed to deficits in visuospatial attention and fixation systems, and/or to their involvement in the saccade initiation (Fischer and Weber 1990; Biscaldi et al. 1994; Chan et al. 2005). However, the latencies in elderly in our study were 250–300 ms in the overlap condition, i.e., much longer than the regular saccadic latency (about 200 ms). Horizontal saccades for elderly showed similar longer latencies (Yang et al. 2005). Latencies of vertical or horizontal saccades in elderly are similar to those of children of 7–8 years old (Yang et al. 2002). Luna and Sweeney (2001) attributed longer latencies in children to the cortical immaturity; there is evidence for cortical degeneration in humans with age (Salat et al. 2001; Head et al. 2004). Thus, in line with these latter studies, we

suggest longer latencies in elderly reflect most likely cortical hypofunction rather than high volitional control. It should be recalled that longer latencies delay the moment for foveating the target, and could interfere with the obstacle avoidance and lead to falling.

Gap effect—express latencies

The differences in mean latencies of vertical saccades between gap and overlap condition, i.e., the gap effect, were equivalent in young and old subjects. More in detail, the percentages of the latency decrease under gap condition (overlap–gap/overlap) were similar in young (29%) and in aged subjects (27%). These results are comparable with those reported for horizontal saccades (Munoz et al. 1998). Findlay and Walker (1999)

proposed that because of the absence of the stimulus during the gap, there was a decrease in fixation activity and thereby an enhancement of movement activity. Munoz et al. (1998) concluded that the gap effect may be the result of several factors together including the disengagement of visual fixation prior to target appearance. In the overlap task fixation is actively engaged at the time of target presentation and its disengagement requires volitional control leading to increase of latencies.

The gap effect is frequently associated with the appearance of express saccades. Such latencies for vertical saccades were observed in monkeys (Bell et al. 2000) and in humans under the gap condition (Goldring and Fischer 1997). Our results also showed express type of latencies under the gap condition, for both young and aged subjects. Overall, the aged subjects seem to present such latencies less frequently than young subjects (12 vs. 16%) but the difference did not reach statistical significance. Furthermore, some aged subjects did show very high rates of express types of latencies (>20%). According to Biscaldi et al. (1996) some subjects called express saccade makers can produce express saccades at rates as high as 30% even in the overlap condition. This is attributed to reduced voluntary control over saccade initiation as a result of poor development of their fixation system. Many other studies in normals showed very low rate or absence of express saccades in the overlap condition (Fischer and Weber 1993; Biscaldi et al. 1996; Munoz et al. 1998). In line with these studies we report very few express saccades (2–5%) in the overlap condition, confirming the normality of the population studied.

In the gap condition, the analysis of the distribution of latency showed a single peak at 120/140 ms for both groups, and provided no evidence for a distinct express peak; other studies reported similar results, e.g., monomodal distributions (Reuter-Lorenz et al. 1991; Wenban-Smith and Findlay 1991; Fischer and Weber 1993). The controversy about the distinct peak is perhaps stronger than the controversy about mechanisms explaining the gap effect. It is believed that express latencies are produced by a hypothetical short cortical circuitry such as retinal–occipital–parietal–super colliculus. The occurrence of minimal latencies between 80 and 120 ms indicates that there is no substantial aging effect in afferent and efferent conduction times; aging seems to affect more central processing.

The effect of eccentricity

For aged subjects latencies of vertical saccades are longer for the eccentricities of 15° than that for 7.5°. For horizontal saccades, lengthening of latency with target eccentricity has been observed but only for extreme values, and was of the order of 0.6–2 ms per degree of saccade amplitude (Baizer and Bender 1989; Becker 1989; Fuller 1996). For example, in the study of Fuller (1996), the latency differences between 10° and 20°

horizontal saccades were not significant but the difference between 10° and 30° was significant as well as between 10° and 40° (8, 22 and 37 ms, respectively). In monkeys, Bell et al. (2000) found that latencies were shorter for vertical eccentricities between 8° and 10°; when stimulus eccentricity was increased further, mean latencies began increasing. However, their report was qualitative and did not show if the latency differences between 8° and 16° of the stimulus eccentricity were significant. In our study, the latencies change little from 7.5° to 15° for young adults (5 ms, no significant). It is mostly for the aged subjects for whom this eccentricity difference appears (32 ms, see Fig. 5a).

Owsley et al. (2000) reported that compared with young adults, the aged subjects showed more localization errors in a task of search of features, and this was accentuated with increasing target eccentricity. They suggested that aged subjects have spatial localization problems, which could be detrimental to the guidance and deployment of visual attention. Bell et al. (2000) also considered that latency increase with larger eccentricity could be due, in part, to sensory factor: as the target eccentricity increases, its location on the retina moves away from the fovea and progressively into an area of reduced visual acuity, which could be more severely affected in aged subjects. As the eccentricity effect in our study is more pronounced for upward targets, one should hypothesize a decline of visual sensitivity asymmetrically distributed for up and down. Visual field studies indicate anisotropic modifications with age (e.g., more accentuated restriction of the upper than down visual field (Haas et al. 1986); such effects may be due to both anatomical restricting, e.g., the excessive upper eyelid skin and shortening of horizontal eyelid fissure (van den Bosch et al. 1999), and/or higher neural processing, as suggested by studies of visual evoked cortical potentials: with aging, the P100 peak latency did not increase for lower half field stimuli, but increased for the upper half field stimuli, especially for smaller check sizes (Sano and Adachi-Usami 1990). Whatever the mechanism is, it should be also noted that the “cost” i.e., the extra time needed for initiation of eccentric upward movements is considerable 32 ms. Thus, orienting gaze in the eccentric upper field becomes more time demanding than elsewhere in aged subjects.

Up/down and distance

The directional asymmetry up/down of latencies of vertical saccades is another interesting topic. The asymmetric latency, with an increase when saccades are elicited to targets in the lower visual field relative to upper targets, has been reported by several authors for adults (Miles 1936; Hackman 1940; Heywood and Churcher 1980; Honda and Findlay 1992; Bell et al. 2000; Zhou and King 2002). Nevertheless, Miller (1969) failed to find significant asymmetry, although for many individuals latencies for downward saccades were

longer. In the study of Goldring and Fischer (1997), four of the six naive subjects and five of the six trained subjects showed decreased latency for upward saccades under the gap condition. In our study, when considering both eccentricities together we did not observe significant difference of latency between upward and downward saccades, although some individual subjects did show such asymmetries.

For horizontal saccades, Yang et al. (2002) reported that latency of saccades at close (20 cm) was shorter than that at far (150 cm) for both adults and children. In this study, we found no overall difference of latencies of vertical saccades between the 40 and 150 cm viewing distance. This is compatible with the study of Honda and Findlay (1992), who found no difference in vertical saccade latency between 30 and 130 cm viewing distance. Yang et al. (2002) discussed the possibility that at close distance attention or fixation disengagement could be more readily released thereby leading to shorter latencies for horizontal saccades. This study shows that such mechanism is not omnidirectional. For vertical gaze shift fixation and attention release are presumably similar regardless of the distance. It should be noted, however, that in the study of Yang et al. (2002) the close distance was 20 cm while in the present study it is 40 cm. Nevertheless, another study of our group indicates latency difference for horizontal saccades between 40 and 150 cm viewing distance (Yang et al. 2005).

In conclusion, the latencies of vertical saccades increase in aged subjects relative to young adults under both gap and overlap conditions. The effect of gap exists for both young and aged subjects and occurs regardless of amplitude, direction and viewing distance. Express type of saccades are produced more under the gap condition than under the overlap condition; they are similarly frequent in young and aged subjects in the gap paradigm while in the overlap paradigm express movements are made rarely and by some subjects only. We suggest that age deteriorates the ability to trigger regular volitional saccades but not the ability to produce express type of saccades. This increase is attributed to the degeneration of oculomotor cerebral areas involved in the initiation of vertical saccades. The results presented here are from aged subjects of exceptionally good health maintaining physical and intellectual activities. Such recruitment allowed to test for the effects of normal physiologic aging in the absence of pathology. We expect that the differences between young and elderly might be even more accentuated for less selective recruitment among elderly. The aged subjects show a latency increase when the target is at larger eccentricity (15° relative to of 7.5°). Neither young adults nor aged subjects show systematic up-down asymmetry in latency of vertical saccades. Distance has no major effect on the latency of vertical saccades.

Acknowledgement Q. Yang was supported by European Union (QLK6-CT-2002-00151: EUROKINESIS) and CNRS/CTI, Handicap contract. L. Ferrufino performed part of the recordings

(DEA diploma, university of Paris V, 2004); D Evelyne Golomer (sports medicine) recruited the aged subjects. The authors thank G. Daunys for programming and electronic help; M. Ehrette for mechanics of the visual display.

References

- Abel LA, Troost BT, Dell'Osso LF (1983) The effects of age on normal saccadic characteristics and their variability. *Vis Res* 23:33–37
- Baizer JS, Bender DB (1989) Comparison of saccadic eye movements in humans and macaques to single-step and double-step target movements. *Vis Res* 29:485–495
- Becker W (1989) The neurobiology of saccadic eye movements. *Metrics. Rev Oculomot Res* 3:13–67
- Bell AH, Everling S, Munoz DP (2000) Influence of stimulus eccentricity and direction on characteristics of pro- and anti-saccades in non-human primates. *J Neurophysiol* 84:2595–2604
- Biscaldi M, Fischer B, Aiple F (1994) Saccadic eye movements of dyslexic and normal reading children. *Perception* 23:45–64
- Biscaldi M, Fischer B, Stuhr V (1996) Human express saccade makers are impaired at suppressing visually evoked saccades. *J Neurophysiol* 76:199–214
- van den Bosch WA, Leenders I, Mulder P (1999) Topographic anatomy of the eyelids, and the effects of sex and age. *Br J Ophthalmol* 83:347–352
- Bucci MP, Kapoula Z, Yang Q, Wiener-Vacher S, Bremond-Gignac D (2004) Abnormality of vergence latency in children with vertigo. *J Neurol* 251:204–213
- Bucci MP, Pouvreau N, Yang Q, Kapoula Z (2005) Influence of gap and overlap paradigms on saccade latencies and vergence eye movements in seven-year-old children. *Exp Brain Res* 164:48–57
- Carter JE, Obler L, Woodward S, Albert ML (1983) The effect of increasing age on the latency for saccadic eye movements. *J Gerontol* 38:318–320
- Chan F, Armstrong IT, Pari G, Riopelle RJ, Munoz DP (2005) Deficits in saccadic eye-movement control in Parkinson's disease. *Neuropsychologia* 43:784–796
- Clarke AH, Ditterich J, Druen K, Schonfeld U, Steineke C (2002) Using high frame rate CMOS sensors for three-dimensional eye tracking. *Behav Res Methods Instrum Comput* 34:549–560
- Coubard O, Daunys G, Kapoula Z (2004) Gap effects on saccade and vergence latency. *Exp Brain Res* 154:368–381
- Creasey H, Rapoport SI (1985) The aging human brain. *Ann Neurol* 17:2–10
- Findlay JM, Walker R (1999) A model of saccade generation based on parallel processing and competitive inhibition discussion (674–721). *Behav Brain Sci* 22:661–674
- Fischer B, Biscaldi M, Gezeck S (1997a) On the development of voluntary and reflexive components in human saccade generation. *Brain Res* 754:285–297
- Fischer B, Gezeck S, Hartnegg K (1997b) The analysis of saccadic eye movements from gap and overlap paradigms. *Brain Res Brain Res Protoc* 2:47–52
- Fischer B, Weber H (1990) Saccadic reaction times of dyslexic and age-matched normal subjects. *Perception* 19:805–818
- Fischer B, Weber H (1993) Express saccades and visual attention. *Behav Brain Res* 57:191–195
- Fuller JH (1996) Eye position and target amplitude effects on human visual saccadic latencies. *Exp Brain Res* 109:457–466
- Gezeck S, Fischer B, Timmer J (1997) Saccadic reaction times: a statistical analysis of multimodal distributions. *Vision Res* 37:2119–2131
- Goldring J, Fischer B (1997) Reaction times of vertical prosaccades and antisaccades in gap and overlap tasks. *Exp Brain Res* 113:88–103
- Haas A, Flammer J, Schneider U (1986) Influence of age on the visual fields of normal subjects. *Am J Ophthalmol* 101:199–203

- Hackman R (1940) An experimental study of the variability in ocular latency. *J Exp Psychol* 27:546–558
- Head D, Buckner RL, Shimony JS, Williams LE, Akbudak E, Conturo TE, McAvoy M, Morris JC, Snyder AZ (2004) Differential vulnerability of anterior white matter in nondemented aging with minimal acceleration in dementia of the Alzheimer type: evidence from diffusion tensor imaging. *Cereb Cortex* 14:410–423
- Heywood S, Churcher J (1980) Structure of the visual array and saccadic latency: implications for oculomotor control. *Q J Exp Psychol* 32:335–341
- Honda H, Findlay JM (1992) Saccades to targets in three-dimensional space: dependence of saccadic latency on target location. *Percept Psychophys* 52:167–174
- Huaman AG, Sharpe JA (1993) Vertical saccades in senescence. *Invest Ophthalmol Vis Sci* 34:2588–2595
- Kingstone A, Klein RM (1993) Visual offsets facilitate saccadic latency: does predisengagement of visuospatial attention mediate this gap effect? *J Exp Psychol Hum Percept Perform* 19:1251–1265
- Klein C, Fischer B, Hartnegg K, Heiss WH, Roth M (2000a) Oculomotor and neuropsychological performance in old age. *Exp Brain Res* 135:141–154
- Klein CH, Brugner G, Foerster F, Muller W, Schweickhardt A (2000b) The gap effect in pro-saccades and anti-saccades in psychometric schizotypes. *Biol Psychol* 55:25–39
- Luna B, Sweeney JA (2001) Studies of brain and cognitive maturation through childhood and adolescence: a strategy for testing neurodevelopmental hypotheses. *Schizophr Bull* 27:443–455
- Miles LK (1936) The reaction time of the eye. *Psychol Monogr* 47:268–293
- Miller LK (1969) Eye-movement latency as a function of age, stimulus uncertainty, and position in the visual field. *Percept Mot Skills* 28:631–636
- Munoz DP, Broughton JR, Goldring JE, Armstrong IT (1998) Age-related performance of human subjects on saccadic eye movement tasks. *Exp Brain Res* 121:391–400
- Munoz DP, Corneil BD (1995) Evidence for interactions between target selection and visual fixation for saccade generation in humans. *Exp Brain Res* 103:168–173
- Owsley C, Burton-Danner K, Jackson GR (2000) Aging and spatial localization during feature search. *Gerontology* 46:300–305
- Pierrot-Deseilligny C, Muri RM, Rivaud-Pechoux S, Gaymard B, Ploner CJ (2002) Cortical control of spatial memory in humans: the visuooculomotor model. *Ann Neurol* 52:10–19
- Pierrot-Deseilligny C, Rivaud S, Gaymard B, Muri R, Vermersch AI (1995) Cortical control of saccades. *Ann Neurol* 37:557–567
- Pratt J, Abrams RA, Chasteen AL (1997) Initiation and inhibition of saccadic eye movements in younger and older adults: an analysis of the gap effect. *J Gerontol B Psychol Sci Soc Sci* 52:P103–P107
- Reuter-Lorenz PA, Hughes HC, Fendrich R (1991) The reduction of saccadic latency by prior offset of the fixation point: an analysis of the gap effect. *Percept Psychophys* 49:167–175
- Rivaud S, Muri RM, Gaymard B, Vermersch AI, Pierrot-Deseilligny C (1994) Eye movement disorders after frontal eye field lesions in humans. *Exp Brain Res* 102:110–120
- Ross LE, Ross SM (1980) Saccade latency and warning signals: stimulus onset, offset, and change as warning events. *Percept Psychophys* 27:251–257
- Ross SM, Ross LE (1981) Saccade latency and warning signals: effects of auditory and visual stimulus onset and offset. *Percept Psychophys* 29:429–437
- Salat DH, Kaye JA, Janowsky JS (2001) Selective preservation and degeneration within the prefrontal cortex in aging and Alzheimer disease. *Arch Neurol* 58:1403–1408
- Sano N, Adachi-Usami E (1990) Aging effects on upper and lower half visual fields by VECs and automated static perimetry. *Nippon Ganka Gakkai Zasshi* 94:527–531
- Saslow MG (1967) Effects of components of displacement-step stimuli upon latency for saccadic eye movement. *J Opt Soc Am* 57:1024–1029
- Schiller PH, Sandell JH, Maunsell JH (1987) The effect of frontal eye field and superior colliculus lesions on saccadic latencies in the rhesus monkey. *J Neurophysiol* 57:1033–1049
- Tzelepi A, Yang Q, Kapoula Z (2005) The effect of transcranial magnetic stimulation on the latencies of vertical saccades. *Exp Brain Res* 164:67–77
- Weber H, Fischer B (1995) Gap duration and location of attention focus modulate the occurrence of left/right asymmetries in the saccadic reaction times of human subjects. *Vis Res* 35:987–998
- Wenban-Smith MG, Findlay JM (1991) Express saccades: is there a separate population in humans? *Exp Brain Res* 87:218–222
- Yang Q, Bucci MP, Kapoula Z (2002) The latency of saccades, vergence, and combined eye movements in children and in adults. *Invest Ophthalmol Vis Sci* 43:2939–2949
- Yang Q, Kapoula Z, Debay E, Coubard O, Orssaud C, Samson M (2005) Prolongation of latency of horizontal saccades in elderly is distance and task specific. *Vis Res* (in press)
- Zhou W, King WM (2002) Attentional sensitivity and asymmetries of vertical saccade generation in monkey. *Vis Res* 42:771–779