

Switching between gap and overlap pro-saccades: cost or benefit?

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Abstract Triggering of saccades depends on the task: in the gap task, fixation point switches off and target appears after a gap period; in the overlap task, target appears while fixation point is still on. Saccade latencies are shorter in the gap task, due to fixation disengagement and advanced movement preparation during the gap. The two modes of initiation are also hypothesized to be subtended by different cortical-subcortical circuits. This study tested whether interleaving the two tasks modifies latencies, due to switching between different modes of triggering. Two groups of healthy participants (21–29 vs. 39–55 years) made horizontal and vertical saccades in gap, overlap, and mixed tasks; saccades were recorded with the Eyelink. Both groups showed shorter latencies in the gap task, i.e. a robust gap effect and systematic differences between directions. For young adults, interleaving tasks made the latencies shorter or longer depending on direction, while for middle-age adults, latencies became longer for all directions. Our observations can be explained in the context of models such as that of Brown et al. (Neural Netw 17:471–510, 2004),

which proposed that different combinations of frontal eye field (FEF) layers, interacting with cortico-subcortical areas, control saccade triggering in gap and overlap trials. Moreover, we suggest that in early adulthood, the FEF is functioning optimally; frequent changes of activity in the FEF can be beneficial, leading to shorter latencies, at least for some directions. However, for middle-age adults, frequent changes of activity of a less optimally functioning FEF can be time consuming. Studying the alternation of gap and overlap tasks provides a fine tool to explore development, aging and disease.

Keywords Saccades · Gap · Overlap · Pure-mixed blocks · Switching tasks · Cortical control

Introduction

Eye movement is a window to study brain function (Zee 2004). In 1967, Saslow first showed different saccade latencies between two different paradigms. In the gap paradigm, the fixation point switched off and target appeared after a gap period; in the overlap task, the target appeared while the fixation point was still on; saccade latencies were found to be shorter in the gap paradigm than in the overlap paradigm. Another important phenomenon could be seen in a gap paradigm: the proportion of very-short latency (80–120 ms) saccades, called express saccades, increased (to 20–30%) (Fischer et al. 1993; Takagi et al. 1995; Goldring and Fischer 1997).

In neuropsychology, several original cognitive tasks have been introduced to evaluate the switching capacity in relation to normal behavior, cognitive aging and pathology. The switching design consists mainly in alternating between two different tasks in the same block of trials

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(mixed block) versus performing each task in separate blocks of trials (pure block). Commonly, a cue indicates shortly before the presentation of the stimulus which type of task the participant has to perform on the stimulus. For example the different tasks can consist in alternating between adding two digits and subtracting two digits (see for instance Belleville et al. 2008). In almost all neuropsychological studies, switch costs were obtained: the reaction time and the percentage of error were higher (a) in mixed blocks compared to pure blocks (global switch cost) and/or (b) inside the mixed block, for switch trials (e.g. task B following task A) compared to non-switch trials (e.g. task B following task B, local switch cost). These costs reflect: (1) maintaining a set of two potentially relevant tasks in working memory; indeed, an “overhead”, i.e. a global controller, is needed to maintain and implement the intention to alternate (Pashler 2000); (2) the online reconfiguration, also called “task set reconfiguration” (Pashler 2000; Belleville et al. 2008), i.e. blocking the set of responses associated with the first task and preparing the set of responses associated with the second task. This reconfiguration is particularly impaired in patients with Alzheimer Disease (Belleville et al. 2008).

In the field of eye movements, the switching capacity has also been studied, mainly using the pro-saccade and the anti-saccade tasks (Slovin et al. 1999; Zhang and Barash 2000; Barton et al. 2002; Cherkasova et al. 2002; Hunt and Klein 2002; Manoach et al. 2002; Bojko et al. 2004; Hodgson et al. 2004; Barton et al. 2006; Cameron et al. 2007; Hikosaka and Isoda 2008). In the pro-saccade task, the participant has to saccade reflexively to the target; while in the anti-saccade task, he or she is asked to direct his/her eyes opposite to the target location. In these studies, a switch cost was found for pro-saccades but for anti-saccades a switch benefit was found most of the time. The two types of eye movements are believed to involve different cortical-subcortical circuits that have been investigated extensively by brain imaging and electrophysiology (for a review, see Leigh and Zee 2006; Johnston and Everling 2008).

The purpose of this study is to examine the existence of a switch cost within the class of pro-saccades, using both the gap and the overlap tasks. To our knowledge, such switching effect was never reported. Most of the time, naive participants are not aware of performing distinct tasks. Our driving-hypothesis is that even though in both tasks the participant has to make a saccade quasi reflexively to the target, the mechanisms of saccade preparation and triggering in the two paradigms may be different. We consequently expect a switch effect to be found when alternating between gap and overlap trials.

This hypothesis is compatible with physiological and behavioral studies providing evidence for earlier fixation disengagement and advanced movement preparation in the

gap task relative to the overlap task (e.g. Dorris et al. 1997; Rolfs and Vitu 2007). Rolfs and Vitu (2007) reported that the advanced movement preparation in gap trials occurs mainly when the uncertainty of target position was low. The hypothesis of different mechanisms is also compatible with several models assuming the existence of different cortico-subcortical circuits subtending triggering for gap and overlap trials (see for instance Isa and Kobayashi 2004; Schiller and Tehovnik 2005). A model of particular interest is the one proposed by Brown et al. (2004). In this model the frontal eye field (FEF) plays an instrumental role for all types of eye movements: different combinations of layers in the FEF, interacting with other cortical and subcortical areas, control different types of saccades such as in gap and overlap trials. Thus, FEF is involved differently for the generation of saccades in gap and overlap trials. We suggest that switching between gap and overlap trials would result in changes in the activity in FEF, leading to a switch effect. Moreover, we suggest that, depending on the age, different functioning of FEF could result in switch cost or benefit.

Another motivation of the present study is methodological, concerning the use of “mixed” versus “pure” experimental design in the investigation of saccades. This study investigates the switching effect between gap and overlap tasks on saccade latencies for all directions of saccades (leftward, rightward, upward and downward) and for two different age groups: young adults (21–29 years) and middle-age adults (39–55 years). We found that for young adults, interleaving tasks shortened or lengthened latencies depending on direction, while for middle-age adults, latencies became longer for all directions. These results are compatible with the idea that the FEF controls differently the preparation and the triggering of the saccades in gap and overlap trials and with the additional assumption of a positive or negative switch effect across lifespan.

Materials and methods

Participants

Ten young adults from 21 to 29 years old (mean 23.7 ± 2.5 years) and ten middle-age adults from 39 to 55 years old (mean 45.0 ± 5.9 years) were tested. The participants were recruited among laboratory collaborators and their family. Two young adults and three middle-aged adults had already participated in eye movements experiments; all other participants were not familiar with saccade tasks. All participants were healthy without any neurological, neuro-otological or ophthalmological symptoms. They had normal or corrected-to-normal vision. Binocular vision was assessed with the TITMUS test of stereoacuity; all individual scores were normal (40" of arc or better). Each

participant gave informed consent to participate in the experiment. This investigation was approved by the local ethics committee and consistent with the Declaration of Helsinki.

Stimuli/visual display

The participant was comfortably seated in an adapted chair with chin rest to stabilize the head. The participant viewed binocularly the visual display, composed of five white luminous dots (angular size $.2^\circ$), presented on a black computer screen placed 57 cm away from the participant. One of these five dots was at the center of the screen, two were at an eccentricity of $\pm 7.5^\circ$ horizontally and two were at an eccentricity of $\pm 7.5^\circ$ vertically.

Oculomotor task

Two paradigms were used: a gap paradigm and an overlap paradigm (Fig. 1). The gap paradigm started by lighting the central dot during approximately 1,500 ms (standard deviation = 100 ms, in order to avoid predictability of the exact moment of the target onset). After this fixation period, the fixation dot was turned off. Following a gap of 200 ms, a target, i.e. one of the horizontally or vertically eccentric dots, appeared for 1,500 ms. The overlap paradigm started by lighting the central dot during approximately 1,700 ms (standard deviation = 100 ms). Then, a peripheral target appeared; both dots were lighted on together during a 200 ms period. Following this overlap period, the central dot disappeared and the peripheral dot remained for another 1,300 ms. Consecutive trials were separated by a period of 1,000 ms with no dot lighted on. The instruction given to the participant was to look at the light dot as accurately and as rapidly as possible.

During each session, the participant performed four blocks. The “pure gap” block contained 60 trials (15 upward saccades, 15 downward saccades, 15 leftward saccades and 15 rightward saccades) of gap paradigm. The “pure overlap” block contained 60 trials (15 toward each direction) of overlap paradigm. The “mixed” block contained 64 trials of either gap or overlap paradigm, with eight trials for each direction and each paradigm. This block was run twice during a session. In each block, the four directions were randomized; in the “mixed” blocks, the two paradigms were also randomized. The order of the blocks was counter-balanced.

Before each block of the oculomotor task, the participant made a sequence of saccades between the white dots, in the four directions; each dot was turned on during 1,000 ms (which is long enough to allow accurate and stable fixation). From these recordings were extracted the calibration factors for each eye.

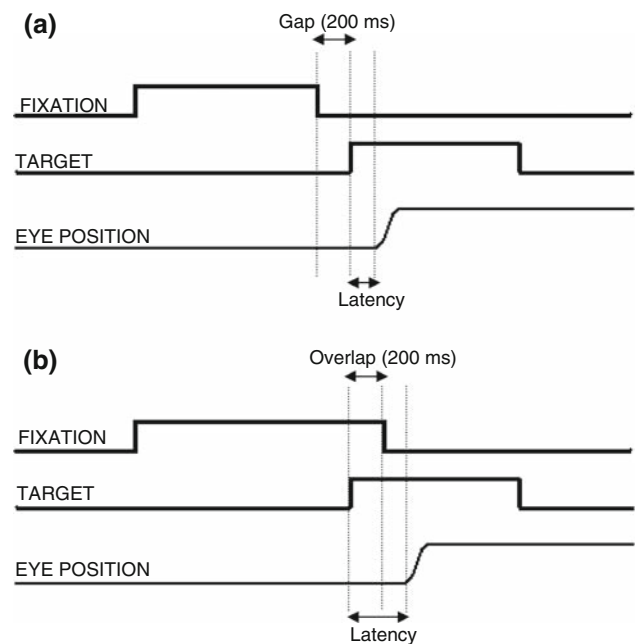


Fig. 1 Experimental paradigms. **a** Gap paradigm, the central fixation point disappeared 200 ms before the appearance of the eccentric target. **b** Overlap paradigm, the central fixation point remained illuminated for 200 ms after the appearance of the eccentric target. In both cases, the latency was the period between the onset of the target and the beginning of the saccade

Eye movement recording

Horizontal and vertical eye movements were recorded binocularly with the EyeLink II device; each channel was sampled at 250 Hz. The system has an accuracy of $.5^\circ$ (absolute position error $<.5^\circ$) and a resolution of $.025^\circ$ (smallest variation of position detectable $<.025^\circ$).

Data analysis

Calibration factors for each eye were extracted from the saccades recorded in the calibration task. A calibration was run on the vertical and horizontal signals with a linear function to fit the calibration data. From the two independently calibrated eye position signals, we derived the horizontal or vertical conjugate signal (mean of the two eye positions). The onset (respectively, the offset) of horizontal or vertical saccades was defined as the time when the eye velocity of the conjugate signal exceeded (respectively, dropped below) 10% of the maximum velocity. Similar criteria have been used in several other studies (Goldring and Fischer 1997; Yang et al. 2002). The automatic placement of the markers by the computer was checked by visual inspection of the individual eye movement traces. From these markers, we measured the amplitude and the latency of saccades.

Altogether, the 20 participants contributed to a total of 4,960 saccade trials; 142 saccades (2.9%) were discarded because they were contaminated by blinks. Among the 4,818 collected saccades, 75 (1.6%) were anticipatory saccades (latency <80 ms), 3 were slow saccades (latency >600 ms) and 3 saccades only (with latency slightly higher than 80 ms) were oriented toward the wrong direction and should rather be classified as anticipatory: thus they were removed from quantitative analysis. The scarcity of anticipation was probably related to the mixing of four directions of saccades within the same block. As all other saccades were toward the correct direction, we can be confident that they were predominantly visually driven saccades.

We calculated the mean latency for each participant in each condition. Four-way ANOVA was applied on latencies to test the effect of the paradigm (gap/overlap), the direction (left/right/up/down), the switching (pure blocks/mixed blocks) and the age (young adults/middle aged adults). Paradigm, direction and switching were the independent variables and age group was the between-group variable. The LSD test of Fisher was then used for post hoc two-by-two comparisons. Finally, an additional analysis was performed to differentiate between global switching effect (difference between trials in pure blocks and non-switch trials in mixed blocks) and local switching effect (difference, inside the mixed blocks, between switch trials and non-switch trials). For instance, a non-switch gap trial is a gap trial following another gap trial; a switch gap trial is a gap trial following an overlap trial. A four-way ANOVA was applied; the factors were paradigm (gap/overlap), direction (left/right/up/down), switching (pure blocks/non-switch trials in mixed blocks/switch trials in mixed blocks) and age (young adults/middle aged adults).

Results

Paradigm, direction, switching and age effects on latencies

Table 1 shows the saccade amplitude for all conditions (the required amplitude was always 7.5°). As saccade latency and saccade accuracy can be interdependent, e.g. the longer the latency, the more accurate the saccade (see van Donkelaar et al. 2007), we first checked the effect of age, paradigm, switching and direction on the amplitude of saccades with a four-way ANOVA. None of these parameters had an effect on saccade amplitude: no main effect and no significant interaction were found ($P < .05$).

Figure 2 shows the mean latencies for each direction in the gap and overlap paradigms and in the pure and mixed conditions for the young adults and for the middle-age adults. The ANOVA (see Fig. 3) showed (a) a significant effect of the paradigm ($F(1, 18) = 96.55$; $P < .001$); (b) a

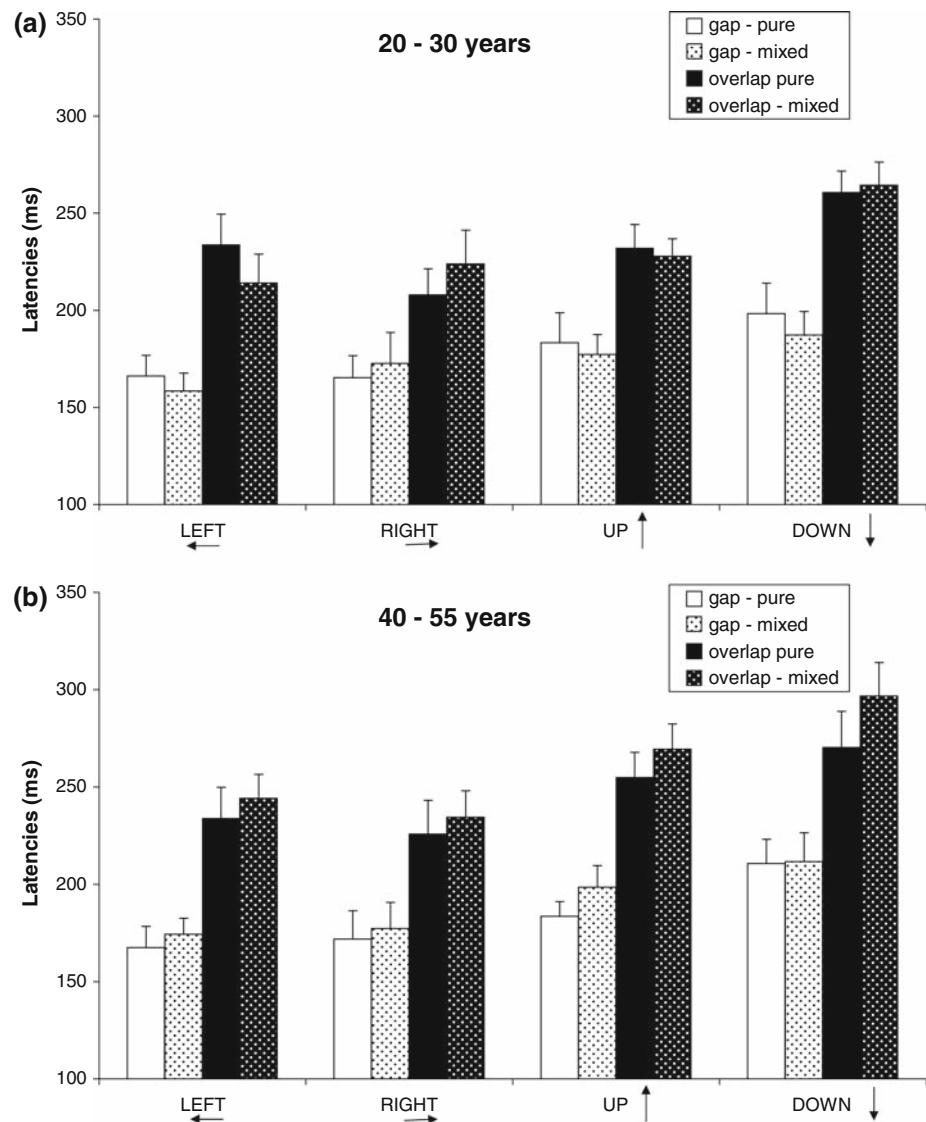
Table 1 Group means and standard errors of the saccade amplitude for each direction (left, right, up, down), paradigm (gap, overlap), block (pure, mixed) and age group (young adults, middle-age adults)

	Pure blocks		Mixed blocks	
	Gap	Overlap	Gap	Overlap
Young adults				
Left	7.1 ± 0.2	6.9 ± 0.3	6.6 ± 0.3	6.6 ± 0.3
Right	6.5 ± 0.4	6.7 ± 0.3	6.5 ± 0.2	6.4 ± 0.2
Up	5.9 ± 0.5	6.3 ± 0.4	5.9 ± 0.3	6.3 ± 0.3
Down	7.1 ± 0.3	7.6 ± 0.5	7.0 ± 0.5	7.2 ± 0.6
Middle aged adults				
Left	7.0 ± 0.2	7.1 ± 0.2	7.3 ± 0.2	7.0 ± 0.2
Right	7.2 ± 0.4	6.8 ± 0.2	7.1 ± 0.2	6.7 ± 0.2
Up	7.0 ± 0.4	6.7 ± 0.4	7.1 ± 0.4	7.4 ± 0.5
Down	7.0 ± 0.4	6.9 ± 0.2	7.0 ± 0.4	7.0 ± 0.6

significant effect of the direction ($F(3, 54) = 12.72$, $P < .001$); (c) a significant interaction between direction and paradigm ($F(3, 54) = 3.13$; $P < .05$); (d) a significant interaction between switching and age ($F(1, 18) = 4.88$, $P < .05$); (e) a significant interaction between direction, switching and age ($F(3, 54) = 3.56$; $P < .05$); and (f) a significant interaction between direction, switching and paradigm ($F(3, 54) = 3.52$; $P < .05$).

The post hoc tests showed the following results: (a) The significant effect of the paradigm was the gap effect: the latencies were 61 ms shorter in the gap than in the overlap paradigm ($P < .001$). (b) The latencies of downward saccades were 22 ms longer than the latencies of upward saccades and 40 ms longer than the latencies of horizontal saccades; latencies of upward saccades were on average 18 ms longer than the latencies of horizontal saccades ($P < .05$). (c) The post hoc analysis for the interaction between direction and paradigm showed that all two-by-two comparisons were statistically significant ($P < .05$) except for the leftward and rightward saccades in the gap trials and for the leftward and rightward saccades in the overlap trials ($P > .05$). (d) The switching had no effect on the latency in young adults when all directions were considered ($P > .05$), but influenced the latency in middle-aged adults (11 ms longer in mixed blocks; $P < .05$). In pure blocks, latencies were similar for both groups ($P > .05$) but in mixed blocks, latencies were 23 ms shorter for young adults ($P < .001$). (e) For young adults, leftward saccades latencies were 14 ms shorter in mixed blocks (switch benefit, $P < .01$) and rightward saccades latencies were 11 ms longer (switch cost, $P < .05$); for middle-aged adults, upward latencies were 15 ms longer in mixed blocks (switch cost, $P < .01$) and downward latencies were 13 ms longer (switch cost, $P < .01$). (f) Rightward saccades

Fig. 2 Group means and standard errors of the latencies for each direction (left, right, up, down), paradigm (gap, overlap) and block (pure, mixed) for the young adults (a) and for the middle-age adults (b)



latencies in the overlap paradigm were 12 ms longer in mixed blocks ($P < .01$) and downward saccades latencies in the overlap paradigm were 15 ms longer ($P < .001$).

In summary, both groups of participants showed a clear gap effect: latencies were shorter in the gap trials than in the overlap trials (Fig. 3a). The effect was similar for middle-age adults (67 ms) and for young adults (57 ms). Secondly, a direction effect existed for both groups: the latencies of downward saccades were longer than the latencies of the saccades in the three other directions and the latencies of upward saccades were longer than the latencies of the horizontal saccades (Fig. 3b). Finally, switching influenced saccade latency differently depending on age, target direction and/or paradigm (interaction switching-age, interaction switching-direction-age and interaction switching-paradigm-direction). These interactions with the switching factor are complex; we will only discuss the most relevant results. Although simplified, in young adults, switch benefit

and cost might exist, whereas in middle-aged adults, only costs were observed (Fig. 3d, e). Moreover, for some directions, switching had different effects on gap and overlap trials (Fig. 3f).

Local and global switching effect

The switching effect may occur at two levels: a local switching effect (difference between switch trials and non-switch trials inside the mixed block) and a global switching effect (difference between non-switch trials inside the mixed block and trials in pure blocks). For instance, a non-switch gap trial is a gap trial following another gap trial; a switch gap trial is a gap trial following an overlap trial. To differentiate the local and global effects, the four-way ANOVA was applied again but with three modalities for the switching factor: trials in pure block, non-switch trials in mixed blocks and switch trials in mixed blocks.

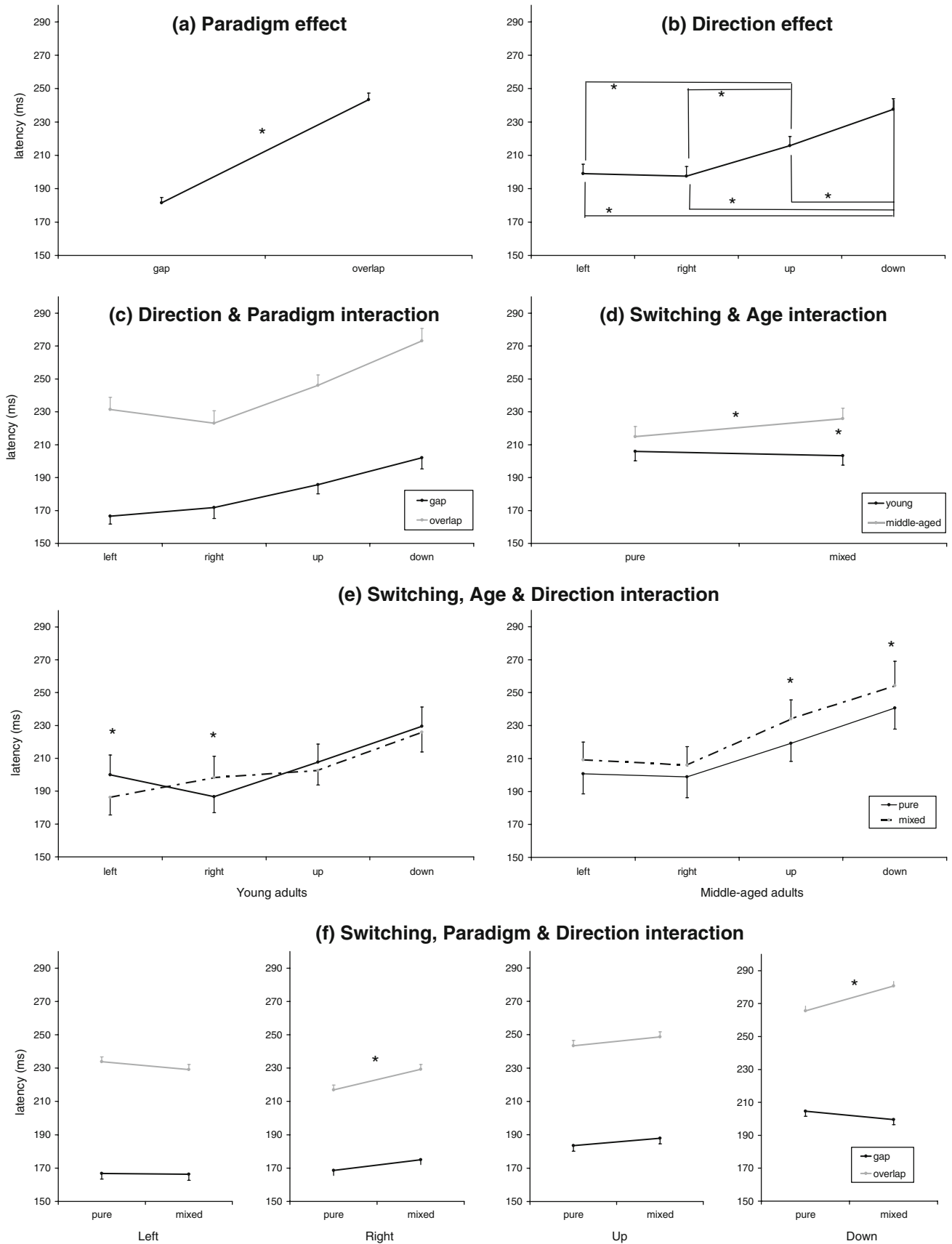


Fig. 3 Significant effects of the first ANOVA (see text) on the latencies. *Asterisks* indicate a statistically significant difference ($P < .05$)

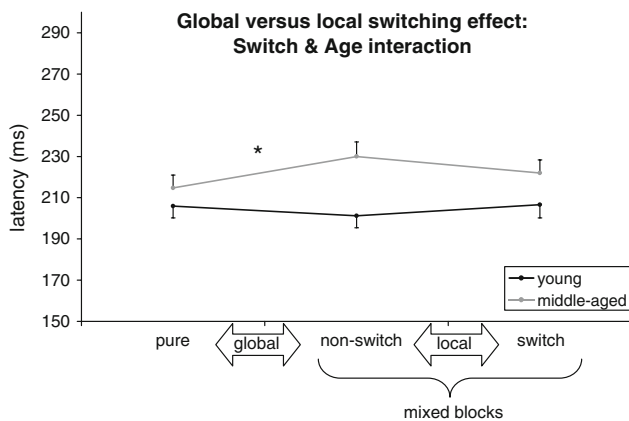


Fig. 4 Significant interaction between age and switching factor on the second ANOVA (see text). *Asterisks* indicate a statistically significant difference ($P < .05$). For young adults there was no evidence for significant switching effect, neither global nor local. In contrast for middle-aged, there was a 15 ms global switching effect and no local switching effect

This analysis confirmed the paradigm main effect (gap effect), the direction main effect and the interaction between paradigm and direction reported in the main analysis. It also showed an interaction between switching and direction ($F(6, 108) = 2.51, P < .05$) and an interaction between switching and age ($F(2, 36) = 5.48, P < .01$). The post hoc test for the interaction between switching and direction showed that a global switch cost and a local switch benefit were found for upward saccades only ($P < .05$). Figure 4 shows the result of the post hoc test for the interaction between switching and age. For young adults there was no evidence for significant switching effect, neither global nor local. In contrast for middle-aged, there was a 15 ms global switching effect ($P < .01$) and no local switching effect.

Discussion

Summary of the results

The main results are the following. (a) A robust gap effect (shorter latencies for saccades in gap than in overlap trials) was present in all conditions. (b) Spatial anisotropies (shorter latencies for horizontal than for vertical saccades, and for upward than for downward saccades) also appeared in all conditions. (c) Switching influenced latencies differently depending on age (young/middle-age), saccade direction (left/right/up/down) and paradigm (gap/overlap).

Robustness of the gap effect

Saslow (1967) was the first to describe the gap effect: shorter latencies in the gap paradigm than in the overlap paradigm. In the present study, a strong gap effect was

found for both young adults and middle-age adults: on average, latency was 61 ms shorter. The gap effect was comparable to that found in elderly (e.g. Yang et al. 2006). Thus, once established during childhood (see Munoz et al. 1998), the gap effect is stable throughout life. This stability reveals specific robust neurophysiological mechanisms.

Different interpretations have been proposed to explain the reduction of mean latency. The theory involving a disengagement of attention during the gap (Fischer et al. 1993; Tam and Stelmach 1993) was rejected (Kingstone and Klein 1993). Instead, a disengagement of the fixation, decreasing the competition between the tendency to fixate new items and the tendency to remain fixated on the current, may occur (Saslow 1967; Kingstone and Klein 1993; Tam and Stelmach 1993; Tam and Ono 1994; Klein et al. 1995) and an advanced movement preparation may take place (Fischer et al. 1993; Klein et al. 1995). Recordings in monkey superior colliculus (SC) showed that fixation-related neurons reduce their activity during the gap period, providing evidence for release of ocular fixation; moreover saccade-related neurons display phasic target-related responses, providing evidence for advanced motor preparation (Dorris et al. 1997). The advanced movement preparation could be a temporal preparation, a state of readiness induced by a warning signal provided by the extinction of the fixation point (Ross and Ross 1980; Ross and Ross 1981; Kingstone and Klein 1993; Findlay and Walker 1999). Rolfs and Vitu (2007) showed that spatial motor preparation contributes to the effect; spatial components are already taken into account during the gap.

Theoretical models suggest that saccades triggered in the overlap task and saccades triggered in the gap task, in particular the express saccades, are produced by different cerebral subcortical circuits. A short circuit, SC–brainstem (Isa and Kobayashi 2004) or occipital cortex–SC–brainstem (the posterior system, Schiller and Tehovnik 2005) plays an important role in the generation of rapid, short-latency saccades in a gap paradigm. The generation of long latency saccades in an overlap paradigm would be controlled by a larger circuit also involving the anterior system (parietal cortex, temporal cortex, FEF) (Isa and Kobayashi 2004; Schiller and Tehovnik 2005).

Spatial anisotropies

In the present study, latencies were shorter for the horizontal directions than for the vertical directions; secondly, latencies were shorter for upward saccades than for downward saccades. These results extend prior studies using only horizontal or vertical saccades (e.g. Honda and Findlay 1992; Goldring and Fischer 1997; Tzelepi et al. 2005); anisotropies are still present when all four directions are interleaved.

Goldring and Fischer (1997) hypothesized that saccade generation is prepared by fixation disengagement (non-directional mechanism) and a spatially selective mechanism which is more or less effective across the visual field. To explain that the horizontal saccades show the shortest latencies, we suggest that reading activity leads to an optimization of the horizontal saccadic system. Tests of populations with different reading systems would be of interest. To explain the up/down asymmetry, Honda and Findlay (1992) suggested a possible association between downward movements and convergence; the preparation of a convergent command may delay the triggering of downward saccades. Tzelepi et al. (2005) explained the asymmetry by a less efficient disengagement of the fixation before a downward saccade and the possible role of the posterior parietal cortex in this fixation disengagement. The less efficient disengagement of fixation for downward saccades could be related to increased capacity of peripheral visual analysis in the lower hemifield, thereby diminishing the necessity for fast triggering of saccades. It has also been speculated that upward saccades could be of shorter latency than downward saccades because of the overall motion of the visual field corresponding to the ground during the walk of a foveated, front-eyed animal. Indeed, such motion causes a downward following eye movement which is then reset by an upward quick-phase eye movement. Such specialization could subserve the advantage of upward saccades (Previc 1990).

In summary, there are spatial anisotropies on saccade latencies in both groups of participants. The exact mechanisms are still unknown; several complementary hypotheses exist but further experiments are needed to test the hypothetical mechanisms.

Switch cost or benefit

The present study shows switch costs and benefits when gap trials and overlap trials are mixed in the same block. To our knowledge, only Coubard et al. (2004) examined the effect of mixing different types of pro-saccades: gap trials were mixed with simultaneous trials (the fixation disappears and the target appears simultaneously, sometimes referred as “0-gap trials”) in the same blocks. Coubard et al. (2004) failed to report a mixing effect on the latencies of saccades. However, in their study, gap trials were interleaved with simultaneous trials and not with overlap trials, probably leading to weaker effect, failing to achieve statistical significance. More importantly, the absence of mixing effect was probably due to the fact that they examined a group of adults heterogeneous in age (18–47 years). Indeed, the most unexpected result in the present study is that in young adults, mixing could speed up initiation of eye movements at least for some directions whereas mixing always slowed down initiation in middle-age adults.

Only a few studies in the literature on task switching reported switch benefit. Jersild (1927), cited by Pashler (2000), reported some switch benefit when using univalent lists. In univalent lists, there are two different types of stimuli, each of them being associated with its own task; in bivalent lists, a same stimulus is associated with different tasks to be accomplished. The existence of switch benefit with univalent lists remains unclear. In the studies of switching between pro-saccades and anti-saccades, a switch cost was found for pro-saccade, but strikingly, a switch benefit was most of the time found for anti-saccade (Barton et al. 2002; Cherkasova et al. 2002; Bojko et al. 2004; Barton et al. 2006). The cost and the benefit varied as a function of cue-to-target interval (Barton et al. 2006), but were not affected by aging (Bojko et al. 2004). Paradoxical cost versus benefit is attributed to inhibition of the saccadic response system by the anti-saccade task; such inhibition would lead to a cost for pro-saccades and a benefit for anti-saccades (Barton et al. 2002; Barton et al. 2006). Another explanation suggests that operation of a second cognitive function requiring attention (task switching) facilitates the execution of non-dominant responses (anti-saccades) and delays usual response (pro-saccades). In the present study, the switch benefit and costs were in the range of 11–15 ms (see Fig. 3e), similar to the range of switch cost and benefit found in other studies with pro and anti-saccades (e.g. Cherkasova et al. 2002). However, none of these two explanations is applicable to the gap and overlap trials used here, both involving pro-saccades.

Many interpretations can be considered for the existence of a switching cost when gap and overlap trials are interleaved. For instance, fixation activity threshold could be overall increased in mixed blocks to avoid anticipatory saccades for overlap trials. Another explanation is that alternating between different triggering mechanisms or distinct subcircuits has a cost, similarly to what is observed in neuropsychological studies, where participants alternate between different cognitive tasks. Note that in the present study, switching effects could be different for gap and overlap trials, at least for some directions (see Fig. 3f); this also supports the existence of different triggering mechanisms for gap and overlap trials. Yet, such interpretations cannot explain both benefit and cost.

Our observations can be explained in the context of models such as those of Isa and Kobayashi (2004) and Brown et al. (2004). Isa and Kobayashi (2004) suggest that different context-dependant collicular activations, in interaction with cortical areas and basal ganglia (BG), play a role in gating cortico-subcortical subcircuits for saccades triggered in gap (in particular short-latency saccades) and in overlap trials. In the TELOS model (Telencephalic Laminar Objective Selector), Brown et al. (2004) proposed a similar idea, more focused on the role of the FEF. In this

model, different combinations of layers in the FEF, interacting with the SC, BG, thalamus, and other cortical areas, would control different types of saccades; for instance, saccades triggered in gap trials and saccades triggered in overlap trials. Thus, according to Brown et al. (2004) the FEF is implicated, even for saccades triggered in gap paradigm.

We suggest that switching between gap and overlap trials would correspond to changes in the activity of different layers within the FEF. The level of activity in the monkey FEF was shown to be related to saccade latency (Hanes et al. 1995; Hanes and Schall 1996). In humans, functional MRI during anti-saccade preparation indicated an increase in brain activation from childhood to adulthood in frontal, parietal, striatal and thalamic regions (Luna et al. 2001). Thus, brain activity depends on age and within adulthood, period of optimal functioning might exist in early adulthood, but this remains to be explored. Relative to the existence of both cost and benefit, one possibility is that in early adulthood, as the FEF is functioning optimally, frequent changes of activity in the FEF can be beneficial, leading to shorter latency (switch benefit). Later in adulthood however, frequent changes of activity in a less optimally functioning FEF can be time consuming (switch cost). Our speculation for benefit in young adults related to frequent switching and optimal function of FEF needs to be further tested.

The finding of a global switch cost for middle aged adults (see Fig. 4) is compatible with the idea of a common structure for controlling saccades in gap and overlap trials. In neuropsychology, a global switch cost is believed to reflect the activation of an “overhead”, i.e. a global controller (see Introduction). Thus a cortico-subcortical network involving the FEF could be the neural equivalent of the concept of a global controller. Rivaud-Pechoux et al. (2007) examined mixing cost in patients with parkinsonian syndromes (Parkinson’s disease, corticobasal degeneration and progressive supranuclear palsy). They compared latency and error rates in pure blocks of pro-saccades or anti-saccades to non-switch trials in mixed blocks (the equivalent of the global switching cost in the present study). They suggest that parietal and frontal cortices and the BG may participate in mixing behavior, particularly impaired in patients with corticobasal degeneration.

In conclusion, switching between gap and overlap trials may delay or speed up latency depending on age and direction. In line with models, we suggest that the activity of a common cortical structure (the FEF, in connection with other cortical and subcortical structures) regulates saccade preparation and triggering differently for gap and overlap trials. From a methodological point of view, it is important to consider the interaction between switching and age. Comparison of latencies between studies should take into account the design of each experiment and the age of the

participants. In addition to theoretical and methodological interests, this study has clinical perspective. Correlations between switch cost or benefit of saccades and neuropsychological tests evaluating mental flexibility are of interest. Indeed, mixing of saccades in gap and overlap trials can be a tool to test switching capacity in various population, e.g. in children or in patients with neurodegenerative disorders. A switching effect between two different types of pro-saccades is interesting, because pro-saccades can be done in almost any population with no particular effort, unlike anti-saccades that require a higher level of cognitive function and cooperation.

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