



Time gaps in mental imagery introduced by competing saccadic tasks

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ABSTRACT

Recently it has been suggested that, somehow similarly to visual saccadic suppression, saccades interrupt some mental activities. After demonstrating that spontaneous eye movements can be used to trace the instantaneous evolution of mental imagery, we show here that making a voluntary saccade or anti-saccade as a secondary task introduces a large delay in a concurrent motion imagery task. An identical task requiring a shift of attention but not saccades also delays imagery, though to a lesser extent. The delay is never compensated afterwards, as if the time dedicated to the secondary task was lost. In contrast, motion imagery is not delayed by spontaneous saccades that accompany imagery, as compared to a fixation condition. We conclude that important time gaps in cognitive activity are introduced only by tasks competing for attentional resources, including voluntary saccades, in dual-task contexts.

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1. Introduction

Compared to other sensory modalities, vision is rather special: due to the frequent alternation of saccades and fixations, the entire visual field is abruptly shifted 2–3 times every second. Yet, normally these visual transients escape conscious perception, and we do not notice discontinuities in the flux of visual information. According to an influential theory, the high-velocity, saccade-related retinal slip would not be perceived thanks to the efference copy of the saccadic motor command, which would partially and transiently inhibit the magnocellular pathway at the time of a saccade (saccadic suppression; Burr, Morrone, & Ross, 1994; Matin, 1974; Ross, Morrone, Goldberg, & Burr, 2001; Stevenson, Volkman, Kelly, & Riggs, 1986), as if motion perception were actively interrupted during saccades. Alternative accounts have instead highlighted the role of retinal signals during saccades. According to some authors, no active suppression of motion perception takes place during saccades (Castet & Masson, 2000). Rather, temporal masking by the pre- and post-saccadic images would be responsible for the sense of continuity in the flux of visual information (Castet, Jeanjean, & Masson, 2002).

Building upon the intuitive notion of visual saccadic suppression, recently it has been proposed that also certain cognitive activities are “suppressed” or slowed during saccadic eye movements. These include counting (Matin, Shao, & Boff, 1993), attention-mediated visual judgments (Brockmole, Carlson, & Irwin, 2002),

memory scanning (Van Duren, 1993), duration estimation (Morrone, Ross, & Burr, 2005), and mental rotation (Irwin & Brockmole, 2000). In these studies, saccades introduced uncompensated time gaps in cognition, with the result that the responses became delayed or inaccurate.

Despite the surface similarity with visual suppression, cognitive suppression may have little to do with its putative parent phenomenon. Firstly, while the former is functional to vision – it contributes to maintain the subjective spatio-temporal continuity of the visual world, cognitive suppression would seem to constitute at least a partial impediment to mental activity. Secondly, cognitive suppression is likely produced by central mechanisms, whereas visual suppression may depend on visual masking mechanisms (Castet et al., 2002). Thirdly, saccades do not always disrupt mental activities. For example, information processing in a primed letter-matching task continues during an intervening instructed saccade (Irwin, Carlson-Radvansky, & Andrews, 1995), probably because the automatic nature of prime processing does not generate any conflict with the concurrent voluntary saccade. Also, saccades were shown to interfere with spatial orientation judgment, because both saccades and spatial orientation would require dorsal stream processing, but not with object recognition, which presumably involves the cortical ventral stream (Irwin & Brockmole, 2004).

Therefore, it appears that cognitive suppression depends on the type of task involved and the context. While the above-mentioned studies emphasized cognitive suppression during saccades, it is likely that there is more to cognitive suppression than mere saccade execution, and that factors other than purely oculomotor factors are involved. These factors may be generally ascribed to

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dual-task contexts, where a conflict between two tasks arises because of a competition for the same central resources (Pashler, 1994; Schubert, 2008). The conflict may arise due to competition for attention resources (e.g., a “conflict of attention”, where shifts of spatial attention require central executive mechanisms, Brisson & Jolicoeur, 2007), but it may also involve other central executive mechanisms (e.g., response selection, Pashler, 1994). Thus, saccades that do not generate a conflict for accessing central resources should produce only a minor, if any, interference with cognitive activity. In this view, most naturally occurring saccades would not be detrimental to cognitive activity, either because they occur automatically or because they are intrinsically planned as part of visual exploratory behaviour (e.g., Land & Hayhoe, 2001). Conversely, tasks that involve deployment of attention should interfere with spatially-based cognitive activity even in the absence of an overt saccade.

Here we explored the interferences produced by various saccadic tasks on a motion imagery task. Because both imagining motion (de’Sperati & Deubel, 2006) and making voluntary saccades (Deubel & Schneider, 1996) involve a deployment of visuospatial attention, we expect a “conflict of attention” to play a major role. The fact that motion imagery is normally accompanied by sequences of spontaneous saccades that mimic in space and time the imagined trajectory (de’Sperati, 2003a, 2003b) offered us the opportunity to study the effects of concurrent saccadic tasks as imagery evolves in “real-time”, and to see when and how time gaps are introduced, as well as whether they are compensated.

2. Methods

2.1. Participants

Fourteen participants (4 males and 10 females, aged between 22 and 28) took part in the experiments, receiving 9 Euro per hour. Five participants took part in Experiment 1, seven in Experiment 2 and seven in Experiment 3. They had normal or corrected-to-normal vision. All but one was naïve as to the purpose of the study. Informed consent was obtained before the beginning of the experiments.

2.2. Stimuli and tasks

2.2.1. Experiment 1

Participants sat in a moderately darkened room, at a distance of 80 cm in front of the computer screen (Sony FD Trinitron, frame rate = 100 Hz, background luminance = 1.1 cd/m²), with the head stabilized with a chin and forehead rest. Each trial (Fig. 1) started with the presentation of a grey central fixation cross (diameter = 0.25°, luminance 10.1 cd/m²) for a random interval between 1000 and 1200 ms, after which it was extinguished. After 50 ms the cross reappeared at 9°, 10.5°, or 12° to the left, and after further 200 ms started moving in the rightward direction at 2, 3, or 4 deg/s velocity. After 1.5 s from motion onset the cross disappeared, so that the stimulus disappeared at 6° left of central meridian of the display for all speed conditions. Participants were instructed to continue motion of the disappeared stimulus in imagery. The cross then reappeared in the right visual field, at 6° of eccentricity, and continued its motion for 1.5 s more before disappearing. In one-third of the trials, randomly selected, the moving stimulus reappeared at the same time at which it would have reached that position had the spot never disappeared (reappearance condition = “Aligned”). In another one-third of trials (reappearance condition = “Behind”), stimulus reappearance was delayed by the time that the stimulus would have taken to move by a further 4° (1 s later for the 4 deg/s speed, 1.5 s for the 3 deg/s and 2 s for

the 2 deg/s speed), while in the last third of trials (reappearance condition = “Ahead”) the reappearance was anticipated by the same amount of time. Participants had to judge whether the spot reappeared ahead of or behind the current position of the imagined moving stimulus (forced-choice response: “Stimulus reappeared ahead”, or “Stimulus reappeared behind”). Two button keys were used for the response. We did not vary the reappearance position nor did we add a random component to the reappearance time, because in a pilot experiment we found that using three fixed reappearance times at the same position was enough to discourage temporal prediction. Thus, we opted for the simpler design, without any random variation of the experimental factors.

2.2.2. Experiments 2 and 3

All task parameters were identical to Experiment 1, except that participants were presented with only 2 deg/s stimulus speed. In addition, participants had to perform a secondary task during the imagery phase (Fig. 1): two grey circular outlines (diameter = 0.33°, luminance 11.9 cd/m²) were displayed throughout the trial, 2° above and below the horizontal trajectory of the moving/imagined spot, and 2° left from the central meridian. After 2 s from the disappearance of the moving stimulus, one of the two circles could turn red (one-third of the trials, luminance = 6.2 cd/m²) or green (one-third of the trials, luminance = 4.8 cd/m²), for 200 ms and then back to grey. In the remaining one-third of the trials the circles remained grey, and participants had simply to continue motion extrapolation (“Control” trials). The three conditions were randomly interleaved. In Experiment 2 the color change was the cue for the participants to make a saccade to that target (green) or an anti-saccade to the other target (red). In Experiment 3 the “Anti-saccade” task was substituted with a “No-saccade” task, in which participants did not have to make the secondary saccade. Importantly, participants were explicitly instructed to maintain the motion imagery despite the intervening secondary task.

In Experiments 2 and 3 there was one condition in which participants were allowed free viewing, without any instruction concerning eye movements (except obviously for the secondary task), and a second condition in which central fixation was required throughout the trial, again except for the secondary task.

2.3. Eye movements recording

Two-dimensional eye movements were recorded with a SRI Generation 5.5 Dual-Purkinje-Image eyetracker with a spatial resolution of about 0.1°. The sampling frequency was 400 Hz, with a 14 bits resolution. Head movements were restricted by an adjustable rest for the chin and the forehead.

2.4. Experimental design and data analysis

In Experiment 1, participants completed four blocks of 45 trials. Each block consisted of 3 reappearance conditions × 3 stimulus velocities × 5 repetitions. In Experiments 2 and 3, participants completed two series of four blocks of 54 trials. Each block combined 3 reappearance conditions × 3 instruction cues (“Saccade”, “Anti-saccade” and “Control” condition without secondary task) × 2 cue positions × 3 repetitions. The two series of blocks were for free viewing and fixation, and were run in sequence. Participants performed Experiments 1, 2, and 3 in sequence, and each block was administered one after another, or in different days or parts of the day, at participants’ convenience. Data distributions were checked for the normality assumption by means of the Kolmogorov–Smirnov test. Percentage data have been subjected to the arcsin square root transformation.

For the statistical analyses, the Student’s *t*-test (both paired and one-sample) was used.

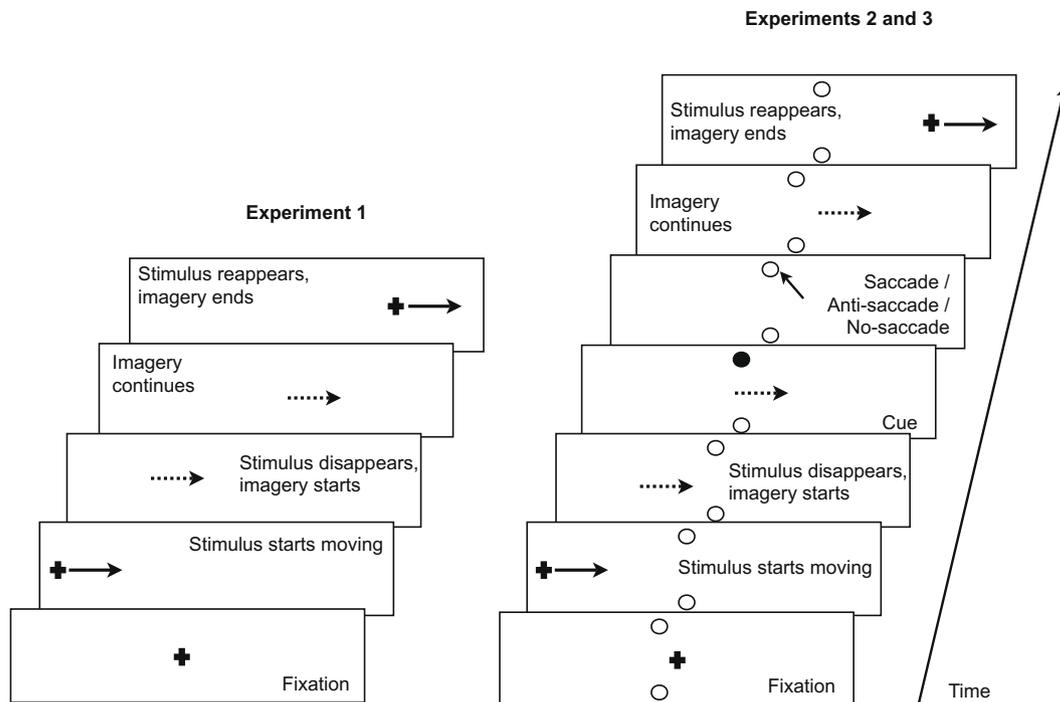


Fig. 1. The task started with the presentation of a central fixation cross. It was extinguished after a random delay and reappeared to the left, where it started moving in the rightward direction with constant velocity. When the moving cross disappeared at 6° to the left of the central meridian, motion imagery started and continued until the cross reappeared 6° to the right of the central meridian. The cross reappeared either at the same time as if it had undergone continuous motion, or with a time lag or lead (not shown, see text). Participants had to indicate whether the cross had reappeared ahead or behind the current position of the imagined moving stimulus. In Experiments 2 and 3 a secondary task was introduced. After 2 s from imagery start one of two targets, located above or below the horizontal trajectory, changed color, as exemplified by the filled circle. Dependent on the color, this was the cue to make a saccade, an anti-saccade, or no-saccade, without interrupting imagery.

3. Results

3.1. Experiment 1: eye movements during mental extrapolation of motion

This experiment was aimed to provide evidence that eye movements can be used as a reliable indicator of dynamic imagery of linear motion, and at the same time to provide baseline measures for Experiment 2 and 3, where participants had also to perform a secondary task during the imagery phase.

Participants had to mentally extrapolate the motion of the moving stimulus after its disappearance, and to press a button according to whether they judged the stimulus having reappeared ahead of or behind the position of the imagined moving stimulus. Typically, participants started following the moving stimulus while visible with smooth pursuit eye movements even though they were not instructed to, and after the object disappeared they spontaneously started a sequence of saccades (Fig. 2A). Visual inspection of the raw eye position traces showed that these sequences of saccades closely followed the imaginary object trajectory. The mean gaze position, obtained by averaging individual eye position traces across trials and participants, reflected the instructed imagery process rather faithfully, showing a clear relation with stimulus velocity (Fig. 2B). The slope of the regression line of the mean gaze position over time (not shown in the figure), evaluated in the interval between 0.5 s after stimulus disappearance and the moment of stimulus reappearance, was 1.94, 2.45, and 3.10 deg/s, respectively for the 2, 3, and 4 deg/s stimulus velocity. Relative to the ideal imagery trajectory (dashed lines), the gaze trajectories had a mean lead of 1.43° , 0.49° and 0.28° , respectively for the 2, 3, and 4 deg/s stimulus velocity. Perhaps due to some underestimation of stimulus speed, the lead tended to decrease gradually over time, eventually reverting to a lag for the 3 and 4 deg/s stimulus velocities.

Speed underestimation most likely resulted from the mixed block design – different stimulus speeds were presented on different trials in the same block – coupled with the relatively short (1.5 s) initial period in which the stimulus was presented as motion template.

Imagery performance was also evaluated independently of oculomotor behaviour. For this, we used two measures, both based on the responses to the reappearance of the stimulus (percentage of “Behind” responses). First, we compared the raw percentage of “Behind” responses in the “Stimulus reappears aligned” condition to the reference value of 50% (chance level, ideal performance). Second, we computed the mean horizontal shift of the logistic function obtained by fitting the percentage of “Behind” responses for the three stimulus reappearance conditions (“Ahead”, “Aligned”, and “Behind”) across all participants. Given that these three conditions correspond to a reappearance spatial shift of -4° , 0° , and 4° , respectively (see the Section 2), the horizontal shift indicates the final lead (if negative) or lag (if positive) of imagery, relative to an ideal imager. Therefore, this value is an estimate of the spatial position of the hypothetical “imagery pointer” at the time of stimulus reappearance. To summarize, a lead in the imagery process would correspond to an increase of “Behind” responses above 50%, associated with a leftward shift of the logistic function. A lag in imagery would result in the opposite pattern.

Across participants, the percentage of “Behind” responses in the “Stimulus reappears aligned” condition was on average 69%, 48% and 48% for the three stimulus velocities (Fig. 3A), suggesting an imagery lead with the 2 deg/s stimulus velocity. However, these values were not significantly different from 50% [for 2 deg/s condition $t(4) = 2.0468$, $p = 0.11$; for 3 deg/s condition $t(4) = -0.2287$, $p = 0.83$ and for 4 deg/s condition $t(4) = -0.3677$, $p = 0.731$, respectively]. The horizontal shift of the logistic function was -1.43° , 0.46° , and 1.15° for the three stimulus velocities, indicating a lead

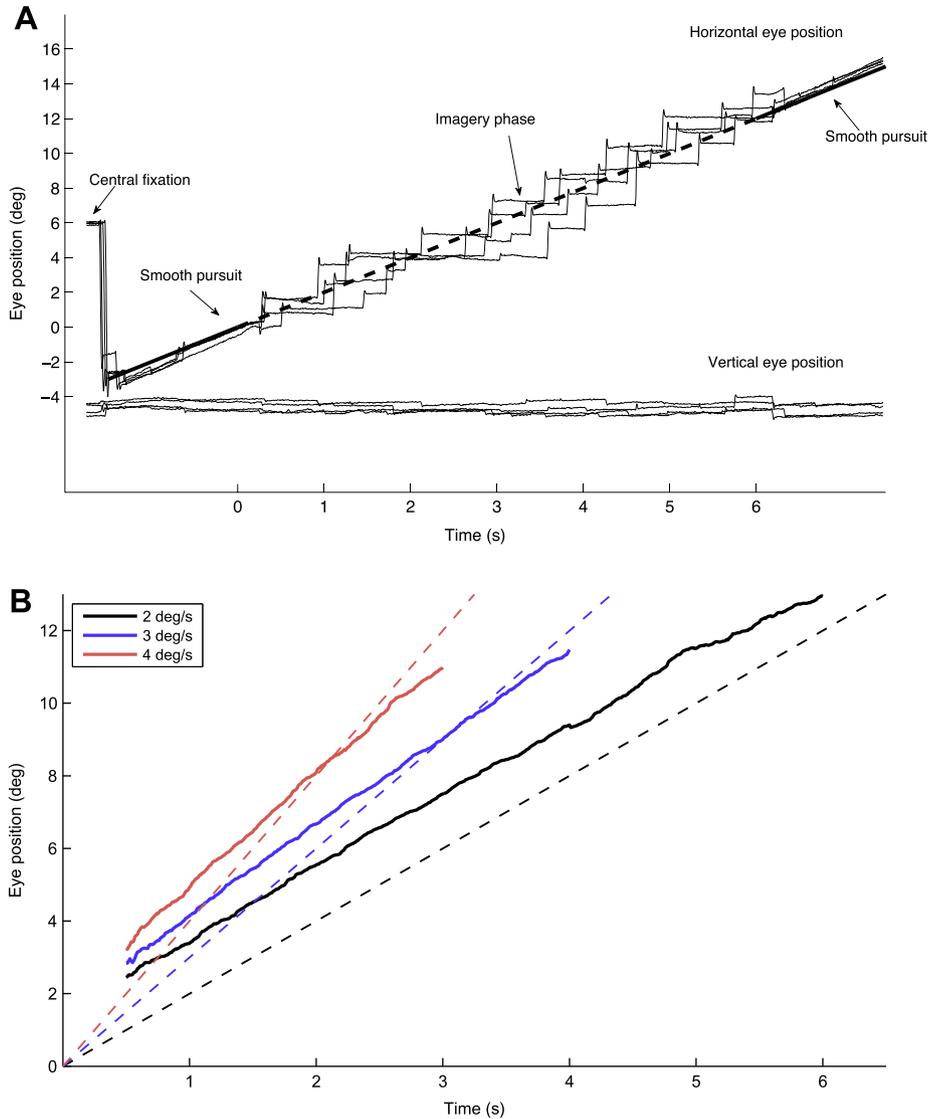


Fig. 2. Eye movements in Experiment 1. (A) Examples of 3 superimposed traces of horizontal and vertical eye position as a function of time from a single participants in a trial, which included initial fixation, smooth pursuit of the motion template, a sequence of saccades during the imagery phase, and a final pursuit phase after the reappearance of the motion stimulus (stimulus speed = 2 deg/s). Participants were given no instruction as to their oculomotor behaviour. Time zero denotes the moment at which the moving stimulus disappears, hence motion imagery starts. The vertical component has been arbitrarily shifted downward for graphical purposes. (B) Mean horizontal eye position as a function of time averaged across trials and participants during the imagery phase for the three stimulus speeds. The oblique dashed lines indicate the ideal imagery trajectory.

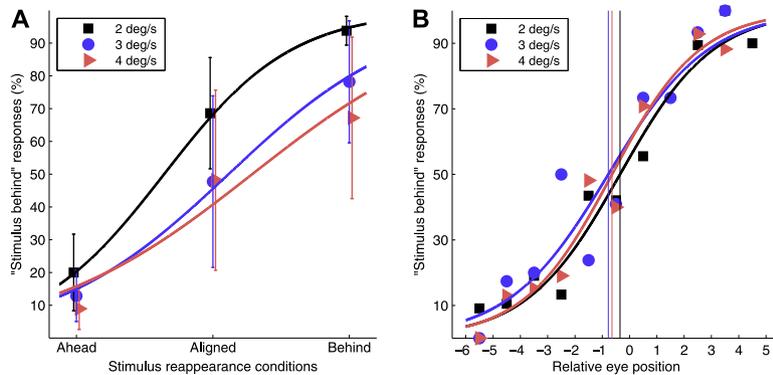


Fig. 3. Imagery performance in Experiment 1. (A) Percentage of “Behind” responses in the “Stimulus reappears ahead”, “Stimulus reappears aligned”, and “Stimulus reappears behind” conditions, together with the logistic plot, for the three stimulus speeds. Error bars represent 95% confidence intervals for the mean across participants. (B) Relation between the proportion of “Behind” responses and the final eye position relative to the stimulus reappearance position. The vertical lines represent the estimated eye position at which the stimulus was judged to reappear aligned with the imagined moving stimulus. Bin width = 1°.

with the stimulus velocity of 2 deg/s, and a lag at the two faster velocities. These data fit nicely the previous results on oculomotor behaviour, at least qualitatively. Overall, these two sources of information (the oculomotor behaviour and the responses to stimulus reappearance) converge to indicate the presence of a final imagery lead with the stimulus velocity of 2 deg/s, and of an imagery lag at the other two stimulus velocities.

We then investigated the relation between the eye position at the time of stimulus reappearance and the probability of giving a “Behind” response. For each trial we took the average value of the horizontal eye position during the 500 ms period preceding stimulus reappearance, excluding the 11% of trials in which a saccade occurred within 100 ms before stimulus reappearance. We then subtracted this mean x -position value from the horizontal position of stimulus reappearance, and thus obtained a relative value representing how much the eyes were leading (positive values) or lagging (negative values) the stimulus reappearance position. These values were then averaged within 11 bins, each 1° wide, in the range -6° to 5° from the stimulus reappearance position, and the percentage of “Behind” responses in these trials computed. Finally, the data-points were fitted with a logistic function in order to recover the x -value corresponding to 50% “Behind” responses (X_{50}), that is, the eye position at which the stimulus was judged to reappear aligned with the imagined moving stimulus. The results are plotted in Fig. 3B, and show a difference of less than 1° between the value of X_{50} and the stimulus reappearance position ($X_{50} = -0.35^\circ, -0.78^\circ, \text{ and } -0.64^\circ$, respectively for the 2, 3, and 4 deg/s stimulus velocities). The negative sign indicates a lag in eye position. Given that the final eye position was in fact taken as the mean eye position during the 500 ms preceding stimulus reappearance, and given the different stimulus velocities, a lag in the eye position of $0.5^\circ, 0.75^\circ, \text{ and } 1^\circ$, respectively for the 2, 3, and 4 deg/s, was expected. The differences between the expected and the estimated values ($0.15^\circ, 0.03^\circ, \text{ and } 0.36^\circ$) were almost negligible. This finding indicates that the gaze position shortly before stimulus reappearance predicted very accurately the imagery performance. In summary, the results of Experiment 1 confirm and extend previous findings that eye movements are a good indicator of mental processes, and that they can be exploited to monitor in real-time the evolution of motion imagery (de’Sperati, 2003a, 2003b).

3.2. Experiment 2: saccade versus anti-saccade

In this experiment we tested the effects of making an instructed saccade or an anti-saccade during motion imagery. In general, the oculomotor behaviour in control trials (i.e., without the instructed saccade or anti-saccade, black traces in Fig. 4A and B) was almost identical to that observed in Experiment 1 for the 2 deg/s velocity condition.

A clear difference in the sequence of horizontal saccades emerged when participants had to make a saccade or anti-saccade during the imagery phase (Fig. 4, red and green traces). When one of the two cues switched to green or red, participants made respectively a saccade to that target, or an anti-saccade to the other target, with a mean latency from cue onset of 497 ± 118 ms SD and 531 ± 127 ms SD, respectively. Given that at the time of color switch the gaze was on average slightly leading the ideal imagery trajectory, the saccade (or the anti-saccade) introduced a small leftward component in the mean horizontal eye position (downward deflection in the horizontal traces). Shortly after the saccade or the anti-saccade, a spontaneous return saccade was made back to the imagery trajectory (mean latency from the offset of the previous saccade: 542 ± 185 ms SD, and 561 ± 203 ms SD for “Saccade” and “Anti-saccade” trials, respectively), after which the sequence of horizontal saccades resumed. The entire process

between the cue color switch and the end of the return saccade took on average 1084 ± 210 ms SD and 1138 ± 233 ms SD, respectively for the “Saccade” and the “Anti-saccade” conditions. Notice that the eyes returned back very close to the same spatial position as before the onset of the first saccade or anti-saccade. In the “Saccade” condition the return saccade landed $0.61 \pm 0.44^\circ$ further to the right relative to the starting position of the first saccade towards the flash; a similar result was observed for the “Anti-saccade” condition ($0.50 \pm 0.48^\circ$); in both conditions this rightward shift was small, but significant (“Saccade” condition, $t(6) = 3.67, p = 0.01$; “Anti-saccade” condition, $t(6) = 2.73, p = 0.03$). Then the sequence of horizontal saccades resumed at the same speed as in the “Control condition” (see below). This introduced a lag in the mean horizontal gaze position relative to both the ideal imagery trajectory and the mean gaze trajectory in the “Control” condition, when no secondary task was required. In Fig. 4C is plotted the lag relative to the “Control” condition, expressed in time units (delay). After 1.5 s from the color switch, that is, when imagery had fully resumed, the delay reached the value of 932 ± 382 ms SD and 957 ± 448 ms SD for “Saccade” and “Anti-saccade” trials respectively. The interruption of the horizontal sequence of saccades was not compensated for in the remaining part of the imagery phase, namely, after the saccade or anti-saccade task. The speed of the mean gaze horizontal position was the same as in the “Control” condition: the slopes of the regression lines computed in the time interval 3.5–6 s for “Saccade” and “Anti-saccade” trials (1.79 deg/s and 1.86 deg/s, respectively) were almost identical to the slope in “Control” trials in the same time period (1.86 deg/s). As a consequence, the delay persisted until the end of the imagery period (mean value in the interval 3.5–6 s: 1055 ± 312 ms SD and 1021 ± 329 ms SD, respectively for “Saccade” and “Anti-saccade” trials, subject-wise).

In “Control” trials, the percentages of “Behind” responses in the condition “Stimulus reappears aligned” was similar to Experiment 1 (62% vs. 69%, black bar, Table 1). Compared to “Control” trials, the percentages of responses were much lower in both “Saccade” (28%) and “Anti-saccade” (35%) trials [$t(5) = -3.9988, p = 0.01$, and $t(5) = -4.653, p = 0.006$, respectively], with no statistically significant difference between the two saccadic conditions [$t(5) = 1.377, p = 0.22$]. The corresponding horizontal shifts of the logistic functions were $-0.81, 1.16, \text{ and } 1.91^\circ$, respectively for the “Control”, “Saccade”, and “Anti-saccade” conditions (Table 1). These data confirm that imagery was delayed by both saccades and anti-saccades, as compared to “Control” trials.

When central fixation was required (Table 1), in “Control” trials the percentages of “Behind” responses in the condition “Stimulus reappears aligned” was smaller but not significantly different from the free viewing condition [43%; $t(5) = 2.376, p = 0.063$]. As in the free viewing condition, the percentages of “Behind” responses decreased when participants had to make a saccade or anti-saccade, as compared to “Control” trials [25%, $t(6) = -4.748, p = 0.003$, and 22%, $t(6) = -3.2895, p = 0.016$, respectively]. The corresponding horizontal shifts of the logistic functions were 0.94, 3.28, and 2.92° , respectively for the “Control”, “Saccade”, and “Anti-saccade” conditions. Thus, motion imagery was delayed by the secondary task also when participants were maintaining central fixation during the imagery period.

Interestingly, at variance with the experimentally imposed saccades or anti-saccades, the presence of spontaneous sequences of saccades was not detrimental to motion imagery, for otherwise imagery would have been faster in the fixation condition than in the free viewing condition. In contrast, there seemed to be a general tendency to slow down imagery when fixation was imposed. In the control trials, the average difference between the horizontal shift of the logistic function in the Fixation and Free viewing conditions amounted to $\sim 1.7^\circ$ (Table 1). By considering that the length of the

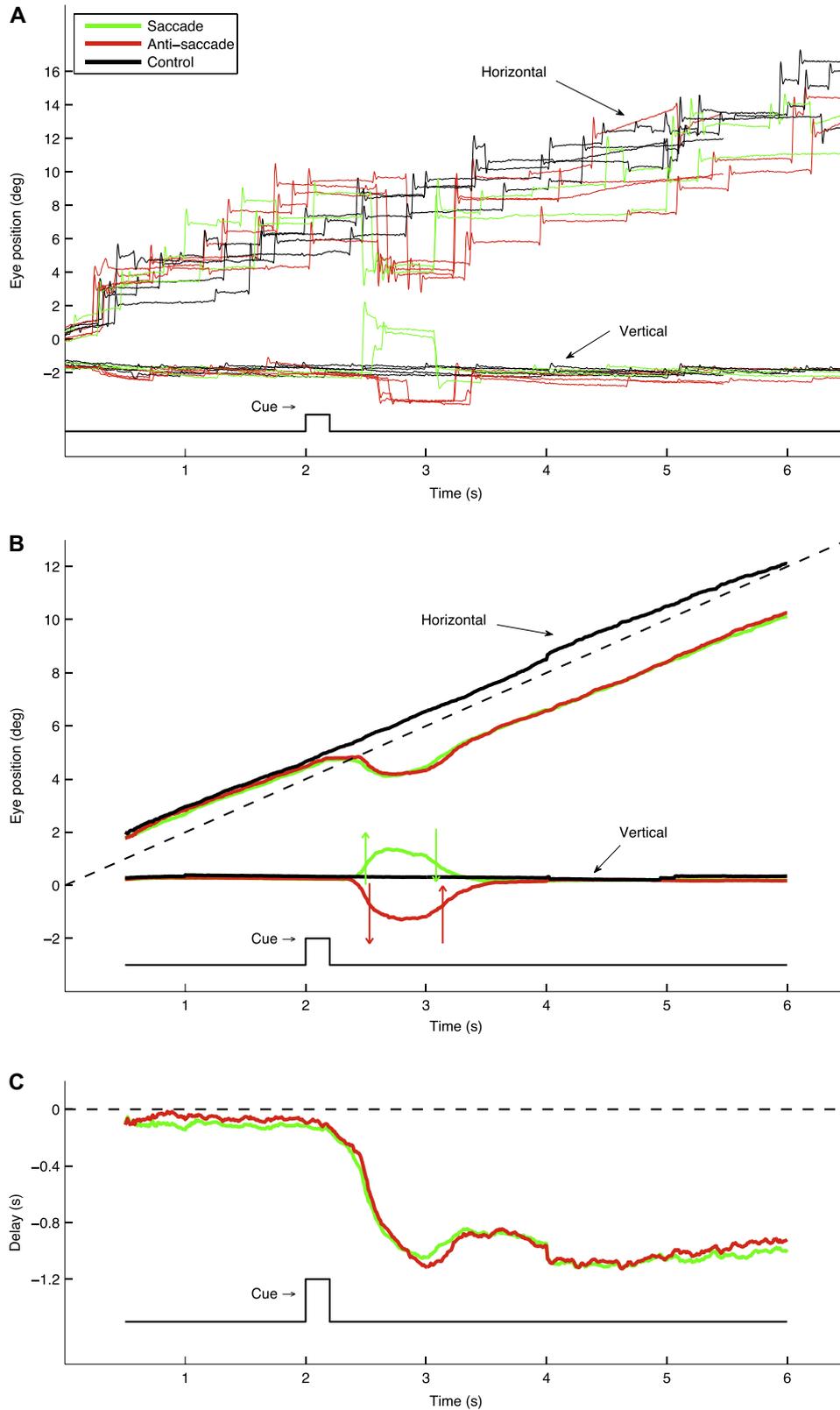


Fig. 4. Eye movements during the imagery phase in “Control”, “Saccade” and “Anti-saccade” trials (Experiment 2). (A) Superimposed traces of horizontal and vertical eye position as a function of time from a single participant. Time zero denotes the moment at which the moving stimulus disappears. The vertical component has been arbitrary shifted downward for graphical purposes. The cue (color change of one target) was not presented in control trials. (B) Mean horizontal and vertical eye position as a function of time averaged across trials and participants. The oblique line indicates the ideal imagery trajectory. The upward green arrow indicates the mean onset time of the saccade in the secondary task, while the downward green arrow indicates the onset of the return saccade. Same for red arrows, but for anti-saccade trials. For graphical purposes, the arrows and the vertical traces are conventionally plotted so that saccades appear directed upward while anti-saccades downward, although in the experiment this factor was counterbalanced. (C) Instantaneous average delay relative to control trials. The delay was computed subject-wise as the time difference between the current eye position in the saccade or anti-saccade condition and the current eye position in the control condition. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Percentage of “Behind” responses in the “Stimulus reappears aligned” condition (P_B) and the corresponding horizontal shift of the logistic function (X_{50}).

	P_B (%)			X_{50} (°)		
	Saccade	Anti-saccade	Control	Saccade	Anti-saccade	Control
Free view	28	35	62	1.16	1.91	-0.81
Fixation	25	22	43	3.28	2.92	0.94

trajectory was 12°, this means that accompanying imagery with eye movements helped by about 14%. This was in keeping with the reported impression of participants of a greater effort in performing fixation trials, as compared to free viewing trials.

3.3. Experiment 3: saccade versus no-saccade

In this experiment we asked whether making a saccadic eye movement was crucial for imagery interruption to occur, or whether it was sufficient that participants were engaged in a secondary task without making a saccade. We ran a second experiment in which, as secondary tasks, participants were asked either to make a saccade (“Saccade” task, as in the previous experiment) or to make no-saccade to the target (“No-saccade” task), according to the color cue. Eye movements in both “Control” and “Saccade” trials were very similar to the corresponding conditions in the previous experiment, with comparable results (Fig. 5A and B). Importantly, an interruption in the horizontal eye position trace was also associated with the “No-saccade” condition. The interruption, however, was shorter than in “Saccade” trials: at 1.5 s from the color switch, the delay in the “Saccade” trials rose to 896 ± 400 ms SD, while in the “No-saccade” trials it was only 246 ± 171 ms SD (Fig. 5C). Both values were significantly larger than zero (always $p < 0.01$), and the difference between them was statistically significant [$t(6) = 4.717$, $p = 0.003$].

Throughout the subsequent imagery phase, the delay accumulated during the “No-saccade” task remained almost constant: the slope of the regression line computed in the interval 3.5–6 s was 1.82 deg/s, a value almost identical to that in “Control” trials (1.88 deg/s). Thus, even though no-saccade was made in the secondary task, there was a clear interruption in the sequence of horizontal eye movements, without any sign of subsequent compensation.

Such interruption did not translate into an equally clear response difference at the end of the trial. In “No-saccade” trials (Table 2), the percentage in the “Stimulus reappears aligned” condition (47%) was higher than in “Saccade” trials [21%, $t(6) = 3.264$, $p = 0.017$], but not significantly lower than in “Control” trials [57%, $t(6) = -1.3464$, $p = 0.227$]. In the fixation condition, there were no differences in the percentage of the responses in the “Stimulus reappears aligned” condition between “Control” and “No-saccade” trials (43% vs. 44%, respectively, for “No-saccade” and “Control” trials, $t(6) = -0.330$, $p = 0.753$, Table 2), while in the “Saccade” trials the decrease was significant (35% vs. 44%, $t(6) = -2.872$, $p = 0.028$). The reason why the imagery interruption in the “No-saccade” trials was clearly visible in the eye movement pattern but not so much in the percentage of response likely depends on the shorter duration of the interruption, compared to saccade trials: a delay of about one-fourth of a second (Fig. 5C) translates into a spatial shift of about 0.5°, which may be too small to be reliably detected through the coarse judgment of the reappearance position.¹ Despite this, the horizontal shifts of the logistic functions re-

flected quite well the delays introduced by the “Saccade” and “No-saccade” tasks in the oculomotor traces (-0.29° , 1.75° , and 0.34° , respectively, for the “Control”, “Saccade”, and “No-saccade” conditions in the free viewing condition, Table 2). The horizontal shifts of the logistic functions indicated consistent delays in the “Saccade” and the “No-saccade” trials, relative to “Control” trials, also in the fixation condition (0.83° , 2.36° , and 1.35° , respectively, for the “Control”, “Saccade”, and “No-saccade” conditions).

4. Discussion

4.1. Saccadic sequences during motion imagery

The primary task in our three experiments was to judge whether a moving spot that disappeared and later reappeared at a new location, had reappeared ahead of or behind the expected stimulus. The eye movement recordings made obvious that this task was not solved by estimating only the time of expected reappearance at the known position; then, we would have expected the participants to perform a single saccade to the known reappearance position, and to wait for the target. Rather, participants performed a sequence of saccades that mirrored the continuous extrapolated target movement, suggesting that the judgment was based on a sort of internal simulation of the continuous motion of the invisible target.

More specifically, our results showed a clear relationship between eye position and imagined motion. During the imagery phase all participants spontaneously made a sequence of saccades, and from the analyses of eye movement traces it seemed that participants were trying to “pursue” the imaginary movement with their eyes. Because smooth pursuit eye movements usually are not elicited in the absence of the stimulus, saccadic – instead of pursuit – eye movements are expected (but see de’Sperati & Santandrea, 2005, for sustained smooth pursuit eye movements during motion imagery). Eye position averaging resulted in mean eye movement trajectories that reflected the speed of the movement to be imagined. Eye movement traces were different for different imagery speeds, but were comparable for the same speed conditions during different experiments. Further evidence that the gaze position reflected imagined stimulus location came from the observation that participants’ judgments about imaginary stimulus location at the end of the trial were very closely related to measured final gaze location.

Several studies have investigated how eye movements could be used to make inferences about mental imagery. For example, it has been shown that participants tend to make systematic eye movements when imagining circular motion of a visual stimulus (de’Sperati, 2003a, 2003b), when imagining arm movements (Gueugneau, Crognier, & Papaxanthi, 2008), when estimating the duration of object falling time (Huber & Krist, 2004), or when recalling visual objects from memory (Brandt & Stark, 1997; Spivey & Geng, 2001). The characteristic signatures of mental rotation were found also in tasks where saccades had to be made to mentally rotated targets, when the visual stimulus was a cue and not the target for the saccade (de’Sperati, 1999; Fischer, Deubel, Wohlschläger, & Schneider, 1999). In these “rotated saccade” tasks, saccadic latency was found to increase linearly with the amount of the imposed angular transformation, which suggested the involvement of a mental rotation process. The distortions introduced by eye movements relative to the underlying motion imagery process are minor, at least with simple motion kinematics (de’Sperati, 2003a, 2003b; de’Sperati & Santandrea, 2005).

These observations naturally pose the question why participants make eye movements and whether eye movements have any functional relationship with imagery. Already some 40 years ago,

¹ We did not expect participants to show the same precision as if they were performing a visual perceptual task. Also, the psychometric function was built on three points only. Pilot observations with more reappearance conditions turned out to involve too many trials for the participants.

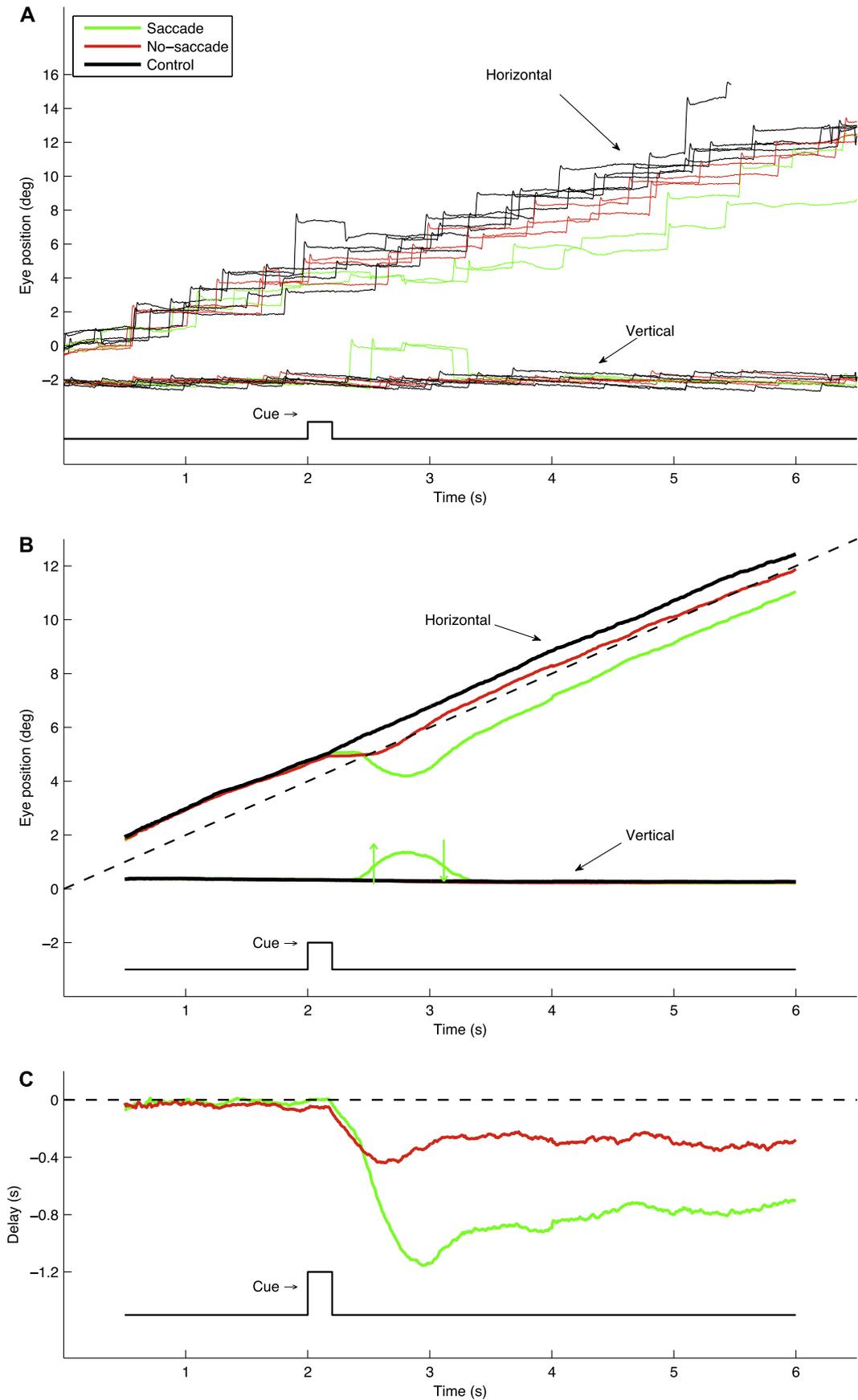


Fig. 5. Same as Fig. 4, but for “Saccade” and “No-saccade” trials (Experiment 3). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Same as Table 1, but for saccade and no-saccade trials (Experiment 3).

	n (%)			X_{50} (°)		
	Saccade	No-saccade	Control	Saccade	No-saccade	Control
Free view	21	47	57	1.75	0.34	-0.29
Fixation	35	43	44	2.36	1.35	0.83

Donald Hebb (1968) proposed that if visual mental imagery is a perceptual-like phenomenon, it should include eye movements. This prediction received multiple experimental support in the past 15 years (see deSperati, 2003a), including evidence for a functional role of eye movements in imagery (Laeng & Teodorescu, 2002). In the latter study, when participants were allowed to move their eyes during object encoding, and then eye movements were restricted during same image recall, participants made more mistakes generating a previously encoded image, than they made with unrestricted eye movements. This suggests that eye movements – even though not necessary – could facilitate imagery. Facilitatory effects of spontaneous eye movements have also been reported in a study by Gueugneau et al. (2008), which showed that participants were faster to execute imagined movement when their eyes were allowed to move as compared to the case when fixation was required. Similar results were reported by Ruggieri (1999), who showed that if participants who are imagining a moving object are forced to stop moving their eyes or their head, motion imagery slowed down or even stopped. Further, the vividness of mental images is significantly reduced when participants simultaneously have to perform an additional visuospatial task, either requiring eye movements or not (Andrade, Kavanagh, & Baddeley, 1997).

We suggest that spontaneous saccades had a functional role for motion imagery. Imagery is experienced subjectively as a faint phenomenon, and this could be one reason why an overt pointer such as eye movements could be helpful. In particular, the sequence of generated eye movements may serve as a spatial pointer that allows a participant to continuously monitor the predicted target position, as an internal simulation of the target movement. This assumption is perfectly in line with the finding that the participants tended to resume motion imagery at just the location where the eyes were after completion of the secondary task (see Figs. 4B and 5B). The tendency for imagery to slow down when fixation was required, as compared to the free eye movement condition, is another sign that eye movements facilitate imagery. Thus, while participants were fixating, they were still able to perform the imagery task, even though they reported that this task was somewhat harder than the free viewing task.

Despite the above considerations, the presence of eye movements in imagery can be interpreted as a bias, instead as a natural facilitation. Thus, for example, it could be that observers' judgments in the imagery task are biased by the current eye position at the time of target reappearance. However, firstly, the delay in the Fixation condition was on average only 5% larger than in the Free viewing condition, as assessed from the shifts of the logistic functions (Tables 1 and 2), which means that the possible effect of eye position at the time of target reappearance was very small. Secondly, regardless of whether eye movements in imagery are interpreted as a bias or a natural facilitation, in our experiments spontaneous saccades did not defer imagery – rather, they slightly speeded it up, which indicates that they did not interrupt motion imagery (see below).

4.2. Secondary attention-demanding tasks interfere with motion imagery

Performing a saccade or an anti-saccade as part of a secondary task delayed motion imagery even though participants were in-

structed to keep on imagining the moving stimulus. A large delay in the mean gaze position built up during the second or so taken to perform the gaze secondary task, after which the eyes resumed the sequence of horizontal saccades. Imagery was delayed irrespective of the fact that participants were allowed free viewing or were keeping the gaze in central fixation, indicating that the delay was not due to interference between two different oculomotor tasks. A smaller but distinct delay in the eye movement traces was introduced when participants did not make any saccade as secondary task, and just decoded the cue, showing that an overt saccade was not necessary to produce the interruption. Again, the time gap was never compensated afterward. The 246 ms delay in the “No-saccade” condition can be taken as an estimate of the duration of the processes associated with the non-motor component of the secondary task.

What causes this marked interference between the imagery task on the one hand and the saccade or attention task on the other? In our view, there are at least three possible theoretical accounts for the interference effects observed here.

First, a temporary interruption of motion imagery may arise from “cognitive suppression” associated with the execution of saccadic eye movements. It has been suggested that mental rotation is suppressed during saccades (Irwin & Brockmole, 2000). Also, decisions on whether pictured items faced to the left or to the right are delayed due to saccades, and visual-spatial processing requiring global/local judgments (Brockmole et al., 2002) were found to be inhibited. Other tasks, such as identity priming (Irwin et al., 1995), word recognition and identification (Irwin, 1998), and object categorisation (Irwin & Brockmole, 2004) continue normally during saccades. From these findings it has been suggested that cognitive suppression occurs because both visuospatial tasks and saccade execution rely primarily on the dorsal pathway. Ventral stream-based operations are not interrupted, as these cognitive tasks do not use the same brain areas that are required for eye movement programming and execution. Indeed, spatial transformations in imagery have been shown to reliably activate parietal regions related to spatial processing (Cohen et al., 1996; Ganis, Thompson, & Kosslyn, 2004; Goebel, Khorram-Sefat, Muckli, Hacker, & Singer, 1998), which supports the claim that they depend on dorsal stream-based processing.

However, we deem it unlikely that our findings result from cognitive suppression. Especially the work of Irwin and Brockmole (Irwin & Brockmole, 2004) has emphasized that cognitive suppression occurs specifically during the execution of saccades. This stems from their observation that the duration of suppression is directly related to the duration of the intervening saccade – larger saccades lead to longer suppression. However, in our “Saccade” and “Anti-saccade” conditions the total duration of the intervening saccades of the secondary task was only about 80–100 ms (two saccades of about 2° each), much too short to account for the long delays that result for motion imagery. Even more important, cognitive suppression due to saccade execution should also result from the spontaneous saccades made during imagery in our experiments. Given that our participants made on average eight saccades per trial, and each of them lasted 30–40 ms, then the expected total suppression duration would be at least 240–320 ms. However, we did not observe any interference when participants made spontaneous saccades during imagery as compared to the central fixation condition, when no-saccades were allowed. Rather, a tendency towards slowing down imagery in the fixation conditions, as compared to the free viewing condition, was seen.

The second and more likely account for interference is related to the fact that saccades and motion imagery compete for common attentional resources. This “conflict of attention” may arise because motion imagery involves a corresponding shift of visuospatial attention (deSperati & Deubel, 2006), and because saccades

and visuospatial attention are tightly coupled (Baldauf & Deubel, 2008; Cicchini, Valsecchi, & de'Sperati, 2008; Deubel & Schneider, 1996; Kowler, Anderson, Doshier, & Blaser, 1995). Strong competition for spatial attention resources occurs in our “Saccade” and “Anti-saccade” tasks when participants are instructed to perform voluntary saccades to the target, at a location that differs from the saccade goal during undisturbed imagery. The same shift of attention, though not followed by overt saccades, resulted in a smaller interference in the “No-saccade” task. Here participants had to only briefly attend to the presented stimulus and make a decision whether to make saccade or not, which correspondingly lead to less interference with motion imagery. The estimated delay was 246 ms, which is close to current estimations of the time taken by allocating visuospatial attention (~200 ms, Castet, Jeanjean, Montagnini, Laugier, & Masson, 2006; see also Deubel, 2008). In our case, a slightly higher value is to be expected due to the additional process of response selection.

Thus, in our dual-task paradigm involving motion imagery and the secondary saccade task there is competition for attentional resources. On the other hand, there should be no interference when saccades spontaneously follow imagery, as there would be a close relation between the attentional spotlight corresponding to gaze location and the one of imagery, which is indeed what we observed. So when the saccades are intrinsic to the imagery task, that is, when they are guided by the same internal process, there is no competition, and no important interference is produced. Only tasks competing for visual-spatial attention are effective in interrupting cognitive activity.

Third, the interference arising from the dual-task situation of our experiments may be of a more general type. People generally have difficulties doing two tasks at once. Dual-task interference has been found with a wide range of tasks, including very easy ones. These findings led to the central bottleneck hypothesis, that is, central processing is dedicated only to one task at a time (Pashler, 1994). Indeed, imagery represents an effortful task, requiring central executive control and attention (Heil, Wahl, & Herbst, 1999; Van Selst & Jolicoeur, 1994). Dual-task costs would then arise from the secondary task since intentional selection of a target and saccade programming would also strain the central bottleneck. For example, response selection is one of the executive processes that typically result in bottleneck interference. It has been shown that the need to select responses for two separate tasks simultaneously results in interference (Ruthruff, Pashler, & Hazeltine, 2003; Tombu & Jolicoeur, 2002), as well as that response selection time increases if more response alternatives are available (Van Selst & Jolicoeur, 1997). Therefore, part of the delay in imagery in our study may have resulted from the need to choose an appropriate response – to make a saccade or an anti-saccade (Experiment 2), or to make a saccade or to ignore the target (Experiment 3).

4.3. Time gaps in imagery are not compensated

Our data showed that there was no compensation for the time taken by the secondary task: the accumulated delay did not diminish, and this was clear both in the mean eye position and in the imagery performance. In principle, there are two possibilities to compensate the delay, which would translate into correspondingly different eye movement patterns: (i) the return saccade of the secondary task may land further rightward relative to the eye position at the time of the first saccade of the secondary task and (ii) the sequence of horizontal sequence may resume at a speed higher than the speed before the interruption in order to reach in due time the display region for the judgment of the reappearance position of the target. These two possibilities are not mutually exclusive. However, none of these strategies was apparent from our data, except

for a very small rightward shift of the return, which was definitely insufficient to compensate for the delay. Why then participants did not compensate the accumulated delay?

One reason could be that participants could not estimate the time dedicated to the secondary task. It is known, for example, that a dual-task condition not only interrupts execution of the primary task, but leaves participants oblivious of the time lost due to secondary task (Brown, 1997, 2006; Brown & Stubbs, 1992; Corallo, Sackur, Dehaene, & Sigman, 2008). Thus, the lack of compensation may be related to the phenomenon of time compression that is known to occur at the time of a saccade. Time compression refers to the fact that the temporal interval between two stimuli presented just before a saccade is reported to be shorter than its objective duration by 50–75 ms (Morrone et al., 2005). Similarly, participants tend to judge events occurring around saccade onset as occurring after it; for example, a visual stimulus displayed just before a saccade is perceived as having occurred some 50 ms later (Morrone et al., unpublished; see also Deubel, Irwin, & Schneider, 1999). In both cases it seems that a short temporal window around saccade onset is lost in the subsequent conscious recall, that is, no compensation takes place. However, although our data also suggest that a temporal window was lost at the time of the secondary task, the delay accumulated in imagery was too large to be explained entirely with this mechanism. A compression of temporal processing comparable in size to the imagery interruption that we have found in the “No-saccade” condition (~250 ms) has been observed to occur when covert visuospatial attention is transiently diverted from a task of temporal duration judgment (Cicchini & Morrone, 2009), suggesting that attention shifts can introduce an important compression in perceived time (see also Macar, Grondin, & Casini, 1994 for a smaller temporal compression with sustained divided attention). The duration of imagery interruption could have been underestimated because timing relies on the same central resources used by other executive-level tasks (Brown, 1997, 2006; Brown & Stubbs, 1992). However, in the above experiments participants were required to make an explicit judgment of the duration of a visual event or to actively produce a temporal interval, while in our case the task was quite different, as participants were urged to continue the imagery task. It is possible that the mechanisms underlying the uncompensated imagery delays that we have observed and those underlying the explicit evaluation of event duration are different.

Another reason for the lack of compensation of the delay could be that participants adopted the less time-consuming oculomotor strategy, i.e., the eyes shifted according to the secondary task and then went back to the very same starting position, thus eliminating the need to calculate a new landing position for the return saccade on the basis of the current position of the imagery trajectory, which in the meanwhile would be shifted further rightward. The computation of new spatial coordinates for the landing position of the return saccade may be a time-consuming process. An analogous argument can be put forth for the possible re-computation of the gaze velocity after the secondary task, an internal operation that would require an additional time. If so, participants could have correctly estimated the time dedicated to the secondary task, but then could not calculate the new gaze velocity without *ipso facto* losing an additional amount of time, with the possible consequence of eventually disrupting the primary task. In this case, the duration of the secondary task might not be really neglected, as instead suggested by previous dual-task studies (Corallo et al., 2008), and the faulty mechanism would be in implementing a compensatory strategy, either by the time of the return saccade and/or during the second part of the imagery phase. The problem, however, seems not to be the re-computation of the gaze trajectory, as this would be at odds with the finding of a comparable imagery lag during fixation condition, where no new trajectory cal-

ulation for eye movements was needed. Clearly, this may just mean that the problem is relative to a general trajectory reconstruction, and not to a specific oculomotor trajectory reconstruction. Also, the lack of compensation was present when no-saccade was requested as secondary task (no-saccade task), which suggests that the problem does not lie at the level of oculomotor execution, but has to do with the allocation of spatial resources (visuo-spatial attention). Further investigation is needed to ascertain whether the lack of compensation of the gap introduced by the secondary task depends on a difficulty of estimating the duration of the lost time or on a difficulty of converting the lost time into an appropriate compensatory strategy.

5. Conclusions

In summary, by reconstructing the instantaneous time-course of motion imagery based on eye movement recordings, we could observe directly the build-up of the delay introduced by a secondary task, both when it involved a saccadic eye movement and when it involved only cue decoding. The accumulated delay was never compensated afterwards, deferring imagery in time by a constant amount. In contrast, motion imagery was not delayed by spontaneous saccades, as compared to fixation trials. Thus the following picture emerges: in a dual-task context requiring a competing covert shift of attention but not saccades, imagery is delayed. Larger delays arise when the secondary task requires a more complex response involving overt saccades. However, no appreciable delays arise when saccades are part of single-task context. Therefore we submit that, out of the ~100,000 daily saccades, only those that are made in the context of a competing secondary task and that do not fit within the natural course of visual exploration introduce important time gaps in cognition.

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