Spatial attention permits to allocate more processing resources to a restricted portion of the visual space. The influential premotor theory states that the allocation of spatial attention relies on the same processes as those responsible for programming saccadic eye movements. Accordingly, several studies have already demonstrated a close spatial correspondence between attention and saccades. However, the question of the temporal coupling between attention displacements and saccades remains unclear. To address this issue, we compared the saccadic latencies to the temporal dynamics of attentional shifts under various cueing conditions known to affect attentional timing. In Experiment 1, we evaluated the effect of peripheral and central cues, and in Experiment 2, we assessed the influence of peripheral cues of different salience levels. We found that the different cue types had a similar effect on saccade latencies and on the dynamics of attentional shifts, either overt or covert. Moreover, even within a given cueing condition, attentional shift times were strongly correlated with saccadic latencies. These results indicate that, in agreement with the premotor theory, both spatial attention and saccades rely on a common process and that the allocation of spatial attention is tightly time-locked to saccade execution.

Keywords: covert attention, overt attention, reflexive attention, voluntary attention, attentional shift, spatiotemporal features


Introduction

Our visual system is continuously confronted with a huge amount of information that our brain is unable to process at once. In order to deal with this myriad of visual inputs, information processing is biased by visual attention, allowing us to focus resources on the most pertinent stimuli, while ignoring the others (Desimone & Duncan, 1995; Treue & Maunsell, 1996). In natural conditions, most of the time, attention shifts “overtly” because it is accompanied by rapid orienting eye movements. However, it has long been demonstrated that we are able to shift our attention “covertly” at a peripheral location, while the gaze remains stationary (Posner, Snyder, & Davidson, 1980). Despite being decoupled from the actual execution of eye movements, covert attentional shifts are strongly linked to saccade preparation, as now supported by numerous psychophysical and neurophysiological studies.

Behavioral evidence for a coupling between attention and saccades

For instance, Sheliga, Riggio, and Rizzolatti (1994, 1995) demonstrated that saccade trajectories deviated away from a covertly attended location, suggesting that the oculomotor circuits were activated concomitantly, but in an infraliminar manner, by attentional shifts. Other psychophysical studies have shown that the locus of attentional shift is confounded with the saccadic land point in overt orienting (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler, Anderson, Dosher, & Blaser, 1995). Besides, attentional...
Evidence for shared neural resources between attention and saccades

Additional support for a tight relation between attention and saccades comes from neurophysiological studies. Indeed, in non-human primates, subthreshold microstimulation studies (Cavanaugh & Wurtz, 2004; Hanks, Ditterich, & Shadlen, 2006; Moore & Fallah, 2001; Schall, 2004), single-unit recording studies (Goldberg, Bisley, Powell, & Gottlieb, 2006; Ignashchenkova, Dicke, Haarmeier, & Thier, 2004), and transient inactivation studies (Lovejoy & Krauzlis, 2010; McPeek & Keller, 2004; Wardak, Ibos, Duhamel, & Olivier, 2006; Wardak, Olivier, & Duhamel, 2002) have emphasized that three brain structures, namely the Frontal Eye Field (FEF), Lateral Intraparietal area (LIP), and Superior Colliculus (SC), known to be involved in the control of saccadic eye movements, also contribute to the control of spatial attention. This was corroborated by transcranial magnetic stimulation (TMS) studies in humans (Chambers, Payne, Stokes, & Mattingley, 2004; Neggers et al., 2007; Taylor, Nobre, & Rushworth, 2007). Finally, fMRI studies have shown overlapping activations in both overt and covert attention conditions (Beauchamp, Petit, Ellmore, Ingholm, & Haxby, 1998; Nobre, Gitelman, Dias, & Mesulam, 2000).

However, despite the large body of evidence supporting the link between attention and saccades, some studies have also challenged this view. Juan, Shorter-Jacobi, and Schall (2004) found that saccades induced by FEF microstimulation were deviated toward the saccade endpoint and not toward the attentional target, suggesting that distinct neural substrates underlie the control of saccades and attentional shifts. Along the same line, distinct cell populations in FEF have been shown to be recruited during attention shifts and saccade preparation (Sato & Schall, 2003; Thompson, Biscoe, & Sato, 2005). In summary, while the existence of a link between attention and saccades is widely accepted, the extent and exact nature of this coupling remain controversial.

The most influential model that accounts for the link between orienting eye movements and attentional allocation is the premotor theory of Rizzolatti, Riggio, Dascola, and Umilta (1987). This theory proposes that attentional shifts are a consequence of saccadic preparation, so that attentional allocation cannot occur without the concurrent preparation of a spatially congruent eye movement. The findings reported above, showing that saccades are always preceded by a spatially specific perceptual improvement strongly supports this theory (Deubel & Schneider, 1996; Kowler et al., 1995).

Temporal coupling between attention and saccades

However, besides the existence of a spatial correspondence between attentional and saccadic targets, the premotor theory also predicts that both mechanisms should be temporally coupled, but evidence supporting this prediction is much sparser. So far, only a few studies have addressed this issue. For instance, in a study in which participants had to perform a dual task involving both saccadic and perceptual tasks, Castet, Jeanjean, Montagnini, Laugier, and Masson (2006) found that the increase in perceptual improvement in the vicinity of the saccadic target, following cue onset, was more pronounced when synchronized with the cue onset than with the saccade onset. This finding suggests that attentional shifts in this experiment exhibited some temporal independence with respect to the saccade execution, being not strictly time-locked to saccade onset. In contrast, Dore-Mazars, Pouget, and Beauvillain (2004) computed the spatial alignment between saccadic land point and attentional allocation as a function of the delay between perceptual target display and saccade onset and found that perceptual performance was maximal at a location corresponding to the saccadic target only when the target was displayed 50 ms before saccade onset. This finding suggests that attentional allocation is conditional on saccadic target location only during the last 50 ms preceding saccade execution and that, outside this time window, attention and saccades can be spatially dissociated. Along the same line, a recent study by Deubel (2008) investigated the time course of attentional allocation in different conditions of congruence between saccadic target and perceptual target locations and he showed that the temporal dynamics of attentional allocation in the vicinity of the saccadic target varied with the experimental conditions, but that in any case, attention was always allocated to the saccadic target location just before the saccade execution. Altogether, these three studies provide an interesting, but incomplete, view on the temporal synchronization between attention and saccades. A critical and untested prediction associated with the hypothesis of a tight synchronization between attention and saccades is that factors influencing the timing of one of these processes should affect the other one in a similar manner. The purpose of the present study was to investigate this question by comparing the effect of different cueing conditions on the time course of both overt and covert attention allocations and on saccadic latencies. We predicted that, if attention is time-locked to...
the saccade onset, the effect of cueing conditions on the
timing of attentional shifts and on saccadic latencies
should be identical.

Experiment 1

An important part of the spatial attention literature is
based on cueing paradigms, relying on stimuli of different
nature to control attentional allocation. In most cases, a
visual cue is presented prior to the target display in order
to direct attention to a given spatial location, either
congruent or incongruent with the target location (Posner
et al., 1980). Two types of cues, either central or
peripheral, are commonly used. Central cues elicit so-
called voluntary attentional shifts, performed according to
the instructions provided by the cue (Posner et al., 1980),
whereas peripheral cues prompt reflexive attentional
shifts, allocated automatically toward the cue location
(Jonides & Irwin, 1981). These two ways of influencing
attentional allocation have led to a distinction between
voluntary and reflexive attentional shifts, which exhibit
dissimilar properties. As far as the temporal dynamics
of attention allocation is concerned, voluntary attention shifts
have been found to be slower than reflexive ones (Carlson,
Hogendoorn, & Verstraten, 2006; Cheal & Lyon, 1991;
Müller & Rabbitt, 1989). In Experiment 1, we aimed to
compare the effect of central and peripheral cues on the
temporal properties of covert and overt attentional shifts
and on saccadic latencies.

Materials and methods

Subjects

Seven healthy subjects with normal or corrected-to-
normal vision participated in Experiment 1. Except for
one author (NF), other subjects were unaware of the
purpose of this study.

Experimental procedures

Stimuli were generated using Matlab 6.5 and Cogent
2000 graphic toolbox. They were displayed on a 21-inch
CRT color monitor (ViewSonic P227f, Sony) with a frame
rate tuned to 100 Hz. Subjects were seated in a dimly
illuminated room, and in order to minimize head move-
ments, a chin and head rest with adjustable straps was
used. The monitor was placed in front of the subject at a
viewing distance of 57 cm. The stimuli sequence
consisted of a fixation frame, a cue frame, a letter frame,
and a visual masking frame (see Figure 1). In the fixation
frame, a central fixation cross (0.4° × 0.4°) was displayed
together with eight evenly spaced rectangles (3° × 3°,
6° eccentricity), filled with random noise dots. These
rectangles were used as forward and backward masks and
as landmarks indicating the location of the upcoming
letters. They were displayed during the whole trial, except
in the letter frame. After a 500-ms delay, the cue was
displayed for 20 ms. In the central cue condition, the cross
was replaced by a central arrow pointing toward the
upcoming target location, whereas in the peripheral cue
condition, a peripheral rectangle was flashed, outlining the
rectangular mask located at the position of the upcoming

Figure 1. Sequence of stimuli in Experiment 1. Trials were triggered upon fixation of central cross. The cue, either a central arrowhead or a
peripheral rectangle, was then flashed for 20 ms. After a variable delay following cue offset, an array of letters was briefly displayed,
including the target (i.e., the cued letter). The stimuli were then replaced by masks. It is noteworthy that the central cross, the cues, and
the alphanumeric characters were displayed in white, and not in black, as shown in the figure for the sake of clarity.
target. The cue was always 100% valid and the cue type remained unchanged during a given block of trials. Subjects were informed about the cue type at the beginning of each block. Only four locations on the display could be cued, marking a 45° angle with respect to the horizontal meridian: upper left, upper right, lower left, and lower right. After the cue presentation and subsequent to a variable cue-target onset asynchrony (CTOA), varying pseudo-randomly from 10, 40, 80, 120 to 160 ms, 8 letters (letter size = 1.4°) were displayed for 50 ms. They were arranged along a virtual circle, appearing at the same location as the masks. The letters were randomly selected in each trial, among a set of 19 letters (D, I, L, O, Q, V, and Z being excluded), and were all different. All the letters were then masked for 10 ms by a whole screen mask (static random noise dots) followed by an array of masks containing the character “8” (size = 1.4°), arranged similarly to the letters and displayed for 750 ms. The purpose of the whole-screen mask was to allow masking during the eye movement execution. Indeed, because of the shift of the image on the retina during eye movements, a mask displayed at the same location as that of a previous visual stimulus will not appear at the same retinal position, thereby preventing masking (Castet et al., 2006). The character “8” masks were found to be effective to prevent visual persistence of letters in a previous study (Zenon, Ben Hamed, Duhamel, & Olivier, 2008).

Subjects were instructed either to fixate the central cross during the whole trial duration (covert condition) or to make a saccade toward the cued letter as soon as the cue appeared (overt condition). In addition, subjects had to perform a perceptual task, which consisted in reporting the cued letter by pressing the corresponding key on a computer keyboard. Given that 19 letters were used, the chance detection performance was 5.26%. Online eye movements were controlled by means of an infrared video camera (ET-49/DALSA camera, Thomas Recordings, Germany) and eye movements were recorded at a sampling rate of 225 Hz; eye position was calibrated at the beginning of each session. An eye movement was considered as a saccade when its acceleration was larger than 2000°/s², a value determined on the basis of preliminary testing. In the covert condition, trials were rejected whenever a saccadic eye movement occurred. In the overt condition, trials were rejected whenever a saccadic eye movement occurred. A trial was considered as valid when (1) the distance between the fixation point and the endpoint of the first saccade was between 4.8° and 7.2°, (2) the angle formed by the saccadic vector (in positive coordinates) and the horizontal meridian was equal to 45 ± 6 degrees, (3) saccadic latency was shorter than 450 ms, and (4) the saccade onset occurred after the target offset. Condition 3 allowed us to ensure the subjects did not favor the perceptual task to the detriment of the saccadic task (Castet et al., 2006). If one of these criteria was not met, the trial was discarded and repeated. Trials in which the saccade was initiated before the letters disappeared (condition 4) were repeated only once. If the second attempt did not satisfy the criteria either, the trial was discarded offline. One of the subjects was excluded from the present analyses because of a too large number of trials discarded offline. For the remaining subjects, the average proportion of trials discarded offline was inferior to 1% in all conditions except for the 120-ms and 160-ms CTOA condition with peripheral cues, in which 12% and 45% of trials were discarded, respectively. In order to insure that this large offline selection of trials did not affect our results, we conducted the relevant analyses both with and without the 160-ms CTOA for the overt peripheral condition. In all cases, removing this condition from the analyses did not affect the results significantly.

Subjects performed four 1-h sessions over 2 days. Each session included 4 pseudo-randomized blocks of 100 valid trials (4 target positions × 5 delays × 5 trials), one for each attentional condition.

Data analyses

The results were analyzed by means of ANOVA for repeated measurements (RM ANOVA). When required, post-hoc comparisons (Tukey tests) were performed. Data expressed as percentages of detection were logit transformed in order to obtain a normal distribution.

To investigate the temporal dynamics of the attentional shifts, data were first normalized so that the maximal performance value among CTOA conditions equaled one. Then, coefficients of a quadratic function were adjusted to fit the logit-transformed data for each subject by means of the Gauss–Newton non-linear fitting procedure (Montagnini & Castet, 2007):

\[
\text{Logit}(p_i) = \log\left(p_i/(1 - p_i)\right) = \beta_0 + \beta_1 x_i + \beta_2 x_i^2, \tag{1}
\]

where \(p_i\) is the proportion of correct response, \(x_i\) corresponds to the corrected CTOA values, and \(\beta_0\), \(\beta_1\), and \(\beta_2\) are the adjusted parameters. Corrected CTOA values correspond to CTOA values to which a constant 25-ms delay is added, thus corresponding to the middle of the display time of the stimulus (CTOA + (stimulus display duration / 2)). The rationale of using a quadratic fitting function is that it allows accounting for a reduction in performance for longer CTOA values, as observed in the peripheral cue condition. We used the inflexion point of this fitted curve, i.e., the point where the first derivative is maximal, as the marker of attentional shift time.

Results

We first compared the temporal dynamics of spatial attentional shifts in the peripheral and central cue...
conditions and in both covert and overt conditions. We performed a three-way RM ANOVA with letter detection performance as dependent variable and with the following independent variables: delay (CTOA; 10, 40, 80, 120, and 160 ms), saccade (covert vs. overt), and cue (central vs. peripheral). We found a significant main effect of these three factors: delay ($F(4,20) = 49.38$, $p < 0.001$), saccade ($F(1,5) = 114.7$, $p < 0.001$), and cue ($F(1,5) = 17.66$, $p = 0.008$). Post-hoc analyses of the delay factor showed a significant performance improvement as CTOA increased (all pairwise comparisons were significant, $p < 0.05$, except between 120 and 160 ms). The main effect of cue and saccade showed a higher rate of cued letter identification in the peripheral than in the central cueing condition ($p < 0.05$), and in the overt than in the covert condition ($p < 0.001$). We also found a significant interaction between delay and cue ($F(4,20) = 8.22$, $p < 0.001$, Figure 2), indicating that performance in both central and peripheral conditions differed only for the shortest CTOA values (Post-hoc analyses: peripheral > central for the three earlier delays, all $p < 0.05$). In contrast, no interaction was observed between delay and saccade ($F(4,20) = 1.43$, ns) or, interestingly, between saccade and cue ($F(1,5) = 1.04$, ns). The lack of significance of the latter interaction suggests that cue type affects attentional allocation equally in covert and overt conditions.

In order to quantify the latency of the attentional shifts in the different experimental conditions, we fitted a quadratic function (see Materials and methods section and Figure 3) to a logistic transformation of the data for each condition and used the timing of the first inflexion point of these functions as an estimate of the attentional shift time ($R > 0.9$ for all fits, see vertical bars in Figure 3). The resulting estimate of the cue effect (central–peripheral) was $18.5 \pm 10.8$ ms and $15.8 \pm 20.8$ ms for covert and overt conditions, respectively. When running an RM ANOVA with attentional shift time as dependent variable and cue type (central vs. peripheral) and saccade condition (covert vs. overt) as independent variables, we found a significant main effect of cue type ($F(1,5) = 8.03$, $p = 0.03$) and not of saccade condition ($F(1,5) = 4.13$, $p = 0.1$). Importantly, the interaction was not significant ($F(1,5) = 0.2$, $p = 0.67$, power $> 0.8$). Conducting the same analysis on the data after discarding the last CTOA value for the peripheral overt condition led to similar results.

We then analyzed the effect of cue type on saccadic latencies. Average cumulative distributions of saccadic latencies are shown for central (purple) and peripheral (pink) cues in Figure 4. Medians of distributions in central and peripheral cue conditions were significantly different (mean $\pm SD$ of the medians for each subject: $239 \pm 10$ ms and $221 \pm 18$ ms, respectively; $F(1,5) = 10.4$, $p = 0.02$).

We compared the effect of cue types on attentional shift times and saccadic latencies by performing an RM ANOVA with saccade/attention (covert attention shift time vs. overt attention shift time vs. saccadic latencies) and cue (peripheral vs. central) as independent variables. As far as the threshold is concerned, we found a significant main effect of saccade/attention ($F(2,10) = 774.6$, $p < 0.0001$), explained by the obvious difference between saccadic latencies and attentional shift times. We also found a significant effect of cue (threshold: $F(1,5) = 12.4$, $p = 0.02$), confirming the difference between peripheral and central cues. Critically, there was no interaction between the cue and saccade/attention factors ($F(2,10) = 0.11$, $p = 0.89$, power $> 0.8$), showing that the cue factor affected identically attentional shift times in both covert and overt conditions and saccadic latencies.

The above results suggest an absence of difference in the effect of cue types between attentional shift time and saccadic latencies. Because of the difficulty in interpreting

![Figure 2. Effect of cue type on the temporal evolution of letter detection performance in covert and overt attentional conditions. Cued letter identification performance is illustrated as a function of CTOA. Error bars represent the mean standard error.](https://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/932795/)
an absence of effect, we tried to confirm a link between attentional shift times and saccadic latencies by showing a significant interaction between these variables. We separated the data into three groups of equal trial number for each subject and for each condition, on the basis of saccadic latencies. We estimated attention shift time by means of the same fitting procedure as previously described (all $R > 0.8$).

We then ran an analysis of covariance with a separate intercept design on attentional shift time data (log transformed) with subject as random factor, cue as categorical factor, and saccadic latency (log transformed) as a continuous predictor. We found a marginally significant effect of saccadic latency on attentional shift time (regression slope: 1.31; $F(1,27) = 3.8, p = 0.06$). The absence of significant interaction between the cue and saccadic latency ($F(1,27) = 1.23, p = 0.27$) indicates that the effect of saccadic latency was similar in both cue conditions (see Figure 5) and that attentional shift times were correlated to saccadic latencies within both cue conditions. Interestingly, because we took saccade latency into account in the model, the cue effect vanished ($F(1,27) = 1.06, p = 0.31$), confirming that, in the overt condition, the variance in the attentional shift time explained by cue type was accounted for by saccadic latency differences.

**Discussion**

In Experiment 1, we found that, in all four attentional conditions, the target letter identification rate increased as a function of CTOA. This finding unveils the displacement of visual attention on the cued location over time and validates the method we used to measure attentional allocation. We replicated the earlier observation that reflexive attentional shifts, triggered by peripheral cues, are faster than voluntary shifts, controlled by central cues (Carlson et al., 2006; Cheal & Lyon, 1991; Muller & Rabbitt, 1989). The main objective of the present experiment was to compare the effect of cue types on covert and overt attentional shifts and on saccade latencies. First, we found that the effect of cue types on covert and overt attentional shifts were similar, suggesting that cue type affects a process that is common to both covert and overt attentional displacements. Second, and most notably, we observed a similar effect of cue types also on saccadic latencies. These results can have three different interpretations: (1) Cue types affect a subprocess that is independent of attention and saccade preparation, such as the process involved in the interpretation of the cue itself, i.e., the transformation of the cue into information.
about the localization of the target for the upcoming attentional and/or saccadic displacement. (2) Cue types affect a single process that is common to covert and overt attentional shifts and to saccadic preparation (i.e., premotor theory). (3) Cue types affect different processes in each of these cases, but its effect on saccades and attentional shifts happens to be similar by chance.

In agreement with the second interpretation, suggesting that attention and saccades share a common subprocess, we found that a large part of the variance observed in overt attentional shift time was accounted for by saccadic latencies and that even in a given cueing condition, the attentional shift times were proportional to saccadic latencies. This covariation of the temporal dynamics of attentional shifts and saccades suggests that a common process is responsible for these variations.

### Experiment 2

In Experiment 1, we demonstrated that the difference in temporal properties between voluntary and reflexive cues was similar for attentional shifts and for saccades. However, the fact that cue types had a similar effect on saccades and attention does not strictly prove that the cues affect a process that is common to saccade and attention, since it cannot be formally excluded that the similitude of the cue type effect is obtained by chance (see above). In order to allow us to strengthen further our conclusion, we attempted, in Experiment 2, to vary saccadic latency while keeping the cue type invariant. To do so, we used cues of different salience values and we compared the influence of the cue salience on the temporal properties of both attentional shifts and saccades. Our prediction was that, similarly to what we found in Experiment 1, the cue salience should influence the temporal dynamics of attention and saccades similarly.

### Materials and methods

#### Subjects

Six healthy subjects with normal or corrected-to-normal vision participated in Experiment 2. All were naive with respect to the purpose of the present study.

#### Experimental procedures

**Main task**

The sequence of stimuli is illustrated in Figure 6. It began with a fixation period varying from 1500 to 1700 ms. Then, a cue frame was shown for 20 ms, containing 12 contiguous peripheral red boxes, located along a virtual circle at an eccentricity of 6 degrees from the center of the monitor screen. One of the boxes played the role of the target cue, which differed from the others (distractors) by its luminance. We varied the cue salience by changing the luminance of the distractors, thereby modifying the difference in luminance between the target cue and distractors. The luminance of the distractors was determined pseudo-randomly and was either 2%, 17%, or 27%
of the maximal screen luminance, whereas the luminance of the target cue was set at 100% of maximal screen luminance. The luminance of the background was fixed at 2% of maximal screen luminance. The target cue randomly appeared in one of the four oblique directions located at 45° angle with respect to the horizontal meridian.

Following the cue offset and after a variable CTOA (10, 20, 40, 80, or 120 ms), 12 white letters (letter size = 1.6 degrees) were displayed for 40 ms at the same locations as the boxes. All the letters from the alphabet were used, except X and M. All letters displayed in a given trial were different, and they were pseudo-randomly selected. The sequence ended with a 10-ms presentation of a random noise dot mask covering the entire monitor screen, followed by an array of masks displayed until the subjects delivered its response. Those masks were presented at the same location as the letters and were built from the superimposition of the alphanumeric characters “8”, “M”, and “X”. These masks were found to be the most effective during preliminary tests, in preventing maintenance of the letters in memory.

Similarly to Experiment 1, subjects had either to maintain their gaze on the fixation point during the whole trial duration or to make a saccade toward the target cue as soon as the cue appeared. In addition, subjects had to report the letter flashed at the location of the target cue by pressing the corresponding key on a computer keyboard. Chance detection performance was 4.17%. The difficulty of this task was adjusted at the beginning of each session by using a staircase procedure, in which the luminance of the letters was varied on an individual basis, so that each subject reached a 60% performance. This staircase procedure was stopped after 48 trials. The luminance value of the letters on which the staircase procedure converged was used for the rest of the experiment. In each attentional condition (covert or overt), 2 blocks of 360 valid trials were run. Block order was pseudo-randomized across subjects.

Saccade direction, amplitude, and latency were controlled online in the overt condition by means of the same infrared video camera as that used in Experiment 1 and by applying the same criteria of detection. Trials were rejected and run again when (1) the amplitude of the first saccade was not in the 6 ± 1.8° range, (2) the saccade was initiated before the letter’s disappearance, or (3) the saccadic latency was longer than 450 ms.

The same analyses as the ones performed in Experiment 1 were applied on the present results.

Results

We first performed a three-way RM ANOVA with letter detection performance as dependent variable and with the following independent variables: delay (CTOA; 10, 20, 40, 80, and 120 ms), saccade (covert vs. overt), and salience (three levels; see Figure 7). We found a significant main effect of delay ($F(4,20) = 100.94, p < 0.001$) and saccade ($F(1,5) = 12.26, p = 0.017$), and a trend leaning toward significance for salience ($F(2,10) = 3.17, p = 0.08$). The only significant interaction was found between delay and salience ($F(8,40) = 5.22, p = 0.0002$; $p > 0.1$ for all other interactions).

We then applied the same fitting procedure to the data as that used in Experiment 1 (see Figure 8). When comparing the resulting attentional shift time estimates (all $R > 0.95$) by means of a two-way RM ANOVA (with salience and saccade as factors), we found a main effect of
salience \((F(2,10) = 13.43, p = 0.001)\) and saccade \((F(1,5) = 7.64, p = 0.04)\). The interaction between saccade and salience was not significant \((F(2,10) = 2.48, p = 0.13, \text{power} = 0.8)\).

The effect of cue salience on medians of saccadic latencies was significant \((F(2,10) = 8.20, p = 0.008)\;\text{cumulative distribution illustrated in Figure 9}\) with latencies of 222.00 ± 33.4, 231.50 ± 21.43, and 258.50 ± 31.97 for first, second, and third salience levels, respectively (mean ± SD of the medians obtained for each subject). We also investigated the effect of cue salience on the dispersion of the saccadic endpoints. We computed the ellipses containing 95% of the saccadic endpoints for each salience condition and compared the surfaces of these ellipses. We failed to find a significant effect of salience on this variable \((F(2,10) = 1.4628, p = 0.28)\). However, the proportion of trials discarded online because of saccade errors (saccades landing on a distractor instead of the target) was slightly higher in the lowest salience condition, even though this effect did not reach significance (RM ANOVA; \(F(2,10) = 3.7144, p = 0.062)\).

Similarly to Experiment 1, the comparison of the effect of cue salience on attentional shift time and saccadic latencies showed no significant difference (RM ANOVA with saccade/attention—covert, overt attention, or saccadic latencies—and salience as independent variables, interaction: \(F(4,20) = 0.98, p = 0.44, \text{power} > 0.8)\).

Finally, as in Experiment 1, we binned the data into three groups of equivalent size according to saccadic latencies. We then conducted an analysis of covariance on attentional shift time (same procedure as before, all \(R > 0.8; \text{log transformed}\)) with subject as random factor, cue salience as categorical predictor, and saccade latency (log transformed) as continuous predictor. Again, we found a clear relationship between saccadic latencies and attentional shift time (regression slope: 1.52; \(F(1,43) = 7.81, p = 0.008)\). The interaction between the effect of saccade latency and cue salience was not significant \((F(2,43) = 0.46, p = 0.63, \text{see Figure 10})\). As in Experiment 1, cue salience was found to have no influence on attentional shift time in this analysis \((F(2,43) = 0.42, p = 0.66)\).

Discussion

The findings of Experiment 2 are twofold. First, we showed that saccade latency and attentional shift times

![Figure 7](https://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/932795/) with saccade/attention—covert, overt attention, or saccadic latencies—and salience as independent variables, interaction: \(F(4,20) = 0.98, p = 0.44, \text{power} > 0.8)\).

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![Figure 8](https://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/932795/) with saccade/attention—covert, overt attention, or saccadic latencies—and salience as independent variables, interaction: \(F(4,20) = 0.98, p = 0.44, \text{power} > 0.8)\).
increase as the salience of the target decreases. Second, we found that the effect of salience on attention and on saccade latencies is identical.

The effect of stimulus salience on saccadic and attentional selection probability has already been extensively studied. It has been shown that conspicuous elements are more likely to be fixated or attended than other items (Parkhurst, Law, & Niebur, 2002; Remington, Johnston, & Yantis, 1992; Theeuwes, Kramer, Hahn, & Irwin, 1998). However, little is known about the influence of salience on the timing of saccade and attentional shift execution. A previous study has already investigated the joint effect of cue luminance and cue validity on the saccadic latency (Kean & Lambert, 2003). In that study, two cues, one bright and one dim, were simultaneously displayed and each cue was associated with a different probability of target occurrence, varied block-wise. Subjects had to make a saccade, as quickly as possible, to the target. In the condition in which the probability of target occurrence was comparable for both cues, the authors reported that bright cues led to faster saccade, indicating that salient cues induce automatic attentional allocation that result subsequently in faster saccades to cued targets. In contrast, in the present study, even though we also found an effect of stimulus salience on saccadic latencies, our interpretation of this finding is dramatically different. Indeed, we show that salient targets directly induce faster saccades, demonstrating that the speed of the processes involved in saccadic target selection, saccade preparation, and/or saccade execution is affected by the target salience.

It is noteworthy that, in the present study, the luminance of the saccadic target was kept constant and that its salience was manipulated by changing the luminance of adjacent distractors. As a consequence, the shorter saccadic latencies observed for salient targets cannot be explained by a mere effect of target luminance.

When distractors are displayed together with a saccadic target, these stimuli compete for selection in oculomotor structures (Dorris, Olivier, & Munoz, 2007; McPeek, 2006). This competition has been evidenced, for example, by showing that saccades deviate from their trajectory when performed in the presence of distractors (McSorley, Haggard, & Walker, 2004). Along the same line, this competition for selection among oculomotor structures could explain the increase in saccadic latencies observed when the contrast between the saccadic target and the distractors decreases. As more salient distractors are added to the display, their corresponding loci of activation in oculomotor structures would inhibit the activity related to the saccadic target and more time would be needed to reach the threshold allowing the onset of the eye movement (Dorris et al., 2007).

Alternatively, it could be assumed that the effect of salience on latency depends on a trade-off between speed and accuracy. If the goal of the oculomotor system is to maintain accuracy as high as possible, an increased difficulty in target selection will result in an increase in latency with minimal effect on accuracy, as found in the present experiment. The slight increase in saccadic error found in the lowest salience condition is in line with this idea. If correct, this hypothesis predicts that under conditions in which latency becomes critical, a decrease in target salience would decrease saccade accuracy without affecting latency. This prediction will require further investigation.

![Figure 9](image_url)

**Figure 9.** Average cumulative distribution of saccadic latencies for the high (blue), intermediate (purple), and low (cyan) salience levels. Colored area indicates the mean standard error.

![Figure 10](image_url)

**Figure 10.** Attentional shift time as a function of saccadic latencies in the three different salience conditions.
Besides, in Experiment 2, we found that attentional shift time was also inversely proportional to the cue salience, and that the effect of cue salience was similar when measured on either overt and covert attention shift times or saccadic latencies. This finding further confirms that attention shifts remain temporally aligned with saccades onset, even when varying the target salience levels.

General discussion

In the present study, we found that the effect of cue types and cue salience on attentional shift times can be accounted for by the effect of these factors on saccadic latency. This result suggests that the different cueing conditions affect a process that is common to both attention and saccadic control. Furthermore, the finding that even for a given cueing condition attentional shift times are strongly correlated with saccadic latencies suggests the existence of a tight temporal coupling between attentional shifts and saccade execution. It could be assumed that this temporal coupling reflects a strategic allocation of spatial attention to the saccadic target before saccade execution, in order to improve accuracy. According to this view, attentional allocation at the saccadic endpoint would not be mandatory, but saccades executed without previous attentional allocation would be simply too inaccurate. However, several studies have reported that even when required to do so, subjects are unable to allocate their attention at a different location from the saccadic target (Deubel & Schneider, 1996), at least during the last 50 ms preceding saccadic onset (Deubel, 2008; Dore-Mazars et al., 2004). Hence, this suggests, as proposed by premotor theory, that the time-locked allocation of spatial attention leading saccade execution is a by-product of the neural processes involved in the programming of the saccade itself.

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