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Title

Time-locked inhibition of covert orienting

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Abstract

It is well known that visual transients can abolish the execution of an eye movement about 90 ms later, a phenomenon known as saccadic inhibition (SI). But it is not known if the same inhibitory process might influence covert orienting in the absence of saccades, and consequently alter visual perception. We measured orientation discrimination performance in 14 participants during a covert orienting task (modified Posner paradigm) in which an uninformative exogenous visual cue preceded the onset of an oriented probe stimulus by 120 to 306 ms. In half of the trials the onset of the probe was accompanied by a brief irrelevant flash, a visual transient that would normally induce SI in an overt task. We report a SI-like time-specific covert inhibition effect in which the irrelevant flash impaired orientation discrimination accuracy only when the probe followed the cue between 165 to 265 ms. The interference was more pronounced when the cue was incongruent with the probe location. We suggest that covert orienting may be susceptible to similar inhibitory mechanisms that generate SI in overt orienting, although the precise time course and mechanisms of this novel effect require further characterisation.

Keywords: covert orienting, visual interference, saccadic inhibition, covert inhibition

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Introduction

The primary function of visual processing is to guide efficient interactions with the surrounding world. This requires us to rapidly integrate new sensory information with ongoing motor behaviour to generate appropriate responses such as inhibiting a previously planned action in order to orient to a novel stimulus. One of the most striking examples of the fast integration of visual information into a motor command is saccadic inhibition (Bompas and Sumner 2011; Buonocore and McIntosh 2008; Buonocore and McIntosh 2012; Edelman and Xu 2009; Reingold and Stampe 1999; Reingold and Stampe 2002). It has been consistently observed that visual transient events interrupt ongoing eye movement behaviour, such that saccades that would otherwise be launched about 90 ms later are inhibited, or delayed. This is visualized as a distinct dip in saccadic frequency around 90 ms after the onset of the visual event, and followed by a rebound period in which the probability of making an eye movement is increased (Reingold and Stampe 2002). Despite being one of the most reliable phenomenon discovered in oculomotor behaviour, the ecological function of saccadic inhibition is not fully understood.

We recently asked whether this interruption of ongoing oculomotor behaviour might have functional benefits in terms of facilitating overt reorienting to a new location in space (Buonocore et al. 2017b). For this purpose, we adapted the well-known double-step paradigm (Becker and Jürgens 1979; Lisberger et al. 1975), asking participants to make an eye movement in response to a sudden-onset visual target, which sometimes jumped to a new location before the first saccade could be launched. Critically, in half of the trials the jump was accompanied by the presentation of a brief (30 ms) visual flash at the top and bottom of the screen. These “flash-jump” trials induced strong saccadic inhibition, and led to a higher rate of successful reorienting to the new target location. We suggested that saccadic inhibition allowed the oculomotor system the time for a decisional process to change response plan. Following this empirical demonstration, new models of saccadic

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inhibition have been proposed, aiming to unify inhibition with the reorienting behaviour observed in countermanding tasks (Bompas et al. 2020; Salinas and Stanford 2018). These findings and models have advanced our understanding of the oculomotor system by suggesting the existence of a common inhibitory signal, driven by new visual onsets, capable of interrupting ongoing orienting behaviour. Nonetheless, they have been concerned exclusively with overt orienting behaviour (saccades), leaving untouched the question of whether covert orienting could be similarly affected.

Despite being fundamental for vision, moving the eyes is not the only way to acquire visual information from the surroundings. Numerous studies have shown perceptual benefits at locations that have been previously cued, even when no eye movement is made, confirming that it is possible to orient attention covertly (Posner 1980; see: Posner 2015 for a review). These studies have mostly used simple detection responses, but covert orienting can also improve the discimination of spatial frequency and lower the contrast threshold for orientation discimination (Barbot et al. 2012; Cameron et al. 2002; Carrasco 2011; Fernández et al. 2019; Lee et al. 1999; Pestilli and Carrasco 2005; Solomon 2004). Given the strong similarities between the overt and covert process, we ask whether the phenomenon of saccadic inhibition, which arises with striking regularity in overt responses, extends to covert orienting behaviour. We operationalised covert orienting in terms of its perceptual consequences, specifically modulations in the ability to discriminate a visual feature (orientation) at a cued or an uncued location. The key question was whether an irrelevant flash, which would induce SI in overt tasks, interferes with perceptual discrimination in a covert task. For this purpose, we adapted our previously-used double-step saccadic task (Buonocore et al. 2017b), to create a novel covert orienting task suitable for testing the inhibitory influence of an irrelevant visual transient. This effectively combined a classic task for the exogenous cueing of covert attention (Posner 1980) with a saccadic inhibition paradigm.

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Materials and Methods

Fourteen participants, aged between 21 and 35 years old (mean = 25.6, *SD* = 3.86), were included in the data analysis. Four additional participants were excluded after the first experimental session, based on poor perceptual performance (see Procedure). All participants were free from neurological and visual impairments. This experiment was conducted in accordance with the British Psychological Society Code of Conduct, with the approval of the University of Edinburgh Psychology Research Ethics Committee.

Apparatus and stimuli

Stimuli were generated using MATLAB R2017b (MathWorks, Inc.) and Psychophysics Toolbox 3.0.14 (Brainard 1997). All the stimuli were in grey scale on a grey background (20.6 cd/m^2), presented on a 19-inch CRT monitor with a refresh rate of 75 Hz (13.3 ms temporal resolution). Participants were seated in front of the monitor at a viewing distance of 79.5 cm with their head on a chinrest and their eyes aligned with the centre of the screen. The fixation point was a small white dot of 0.05 degrees radius (84.9 cd/m^2). The cue was a filled white circle of 0.2 degrees radius at full contrast (84.9 cd/m^2), at an eccentricity of 10 degrees from the fixation point and 1.5 degrees above the centre of the possible probe location on that side (e.g. Pestilli and Carrasco 2005). The probe stimulus was a tilted Gabor patch with a radius of 0.55 degrees, a contrast of 0.2 and a spatial frequency of 1.78 c/deg, 10 degrees to the left or right of the fixation point. Eye movements were monitored with a tower-mount Eyelink 1000 system tracking the right eye, at a sampling rate of 1000 Hz. Manual responses were recorded by button presses on a custom response pad. The room was dark, except for the display monitor, and the operator monitor located behind the participant and facing away from them. Each

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participant completed two testing sessions on separate days lasting about one hour each including breaks. The first testing session involved a practice block, a QUEST procedure for orientation threshold (repeated up to three times), and 19 blocks of experimental trials. The second testing session comprised only the 19 blocks of experimental trials.

Procedure

At the beginning of each experimental testing session, the practice block and the QUEST procedure, a 9-point calibration was conducted. Calibrations were repeated if the average error across all points was greater than 0.5 degrees, and after every 200 trials. In both the QUEST and the main experimental trials, participants were instructed to fixate the fixation point at the centre of the screen throughout the trial and to report the orientation of the Gabor patch (left or right tilted) by pressing with the button under their left or right index finger respectively. We used discrimination of orientation so that the exogenous cue was orthogonal to the features of the stimulus, providing a measure of modulations in sensitivity. Speed of responding was not emphasised. If participants moved their eyes outside of a fixation window of 3 degrees radius, the trial was aborted and randomly reshuffled into the remaining trial sequence.

At the start of the experimental procedure in the first session, to familiarise with the basic task, participants first performed a practice block of 16 trials in which the onset of a cue was followed after a random delay by the onset of a probe at the same spatial location (congruent cue condition). The practice block was followed by a QUEST staircase procedure (Watson and Pelli 1983) to identify a suitable orientation per participant that avoided floor or ceiling levels of discrimination. The trial sequence for the QUEST followed the same structure as the subsequent experimental trials (description below), for a maximum of 80 trials, but only congruent cue conditions were used. The QUEST parameters were set to a 75% performance criterion, a beta of 1.5, and a grain of 1. If the

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estimated threshold orientation was greater than 15 degrees, the QUEST was run again up to a maximum of three times. Participants were excluded from the main experiment if they still had an outcome greater than 15 degrees after the third QUEST, or if at the end of the whole first session their average performance in experimental trials was below 60%. Four participants were excluded on this basis.

The experimental task was an adaptation of the classic cue Posner paradigm for covert perceptual judgements, modified to mimic the structure of Experiment 3 in Buonocore et al. (2017b) for overt eye movement responses (Fig. 1A). Each trial began with the onset of a white fixation dot. After a random interval between 800 ms and 1200 ms, the cue was presented for 53.3 ms to the left or right of fixation. The probe was presented for 106.6 ms after a cue-target onset asynchrony (CTOA) determined at random between 120 and 306.6 ms, with equal numbers of trials at the cued location (*congruent cue condition*) or at the uncued location (*incongruent cue condition*). On half of the trials, a black flash (0.34 cd/m^2) covering the bottom and top thirds of the screen was presented for 13.3 ms simultaneously with the onset of the probe. This technique was introduced by Reingold and Stampe (2002) as a way to induce saccadic inhibition without interfering with the localization of a saccade target. It was recently adapted to saccade tasks requiring a concurrent perceptual response (Buonocore et al. 2016; Buonocore and Melcher 2015), establishing a lack of masking effects of this remote flash on probe perception. It is interesting to note that although the flash was a salient change, it was extremely brief, and most participants on questioning did not notice it at all.

The main experiment had four probe conditions: congruent (25%), congruent plus flash (25%), incongruent (25%) and incongruent plus flash (25%). Participants completed a total of 38 blocks of experimental trials across the two test sessions. Within each block, there were 16 trials, four trials per probe condition by two probe locations (left and right)

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and two probe tilts (left and right). Each participant thus completed a total of 1216 valid trials, resulting in 304 trials per probe condition (collapsed across side, tilt, and CTOA).

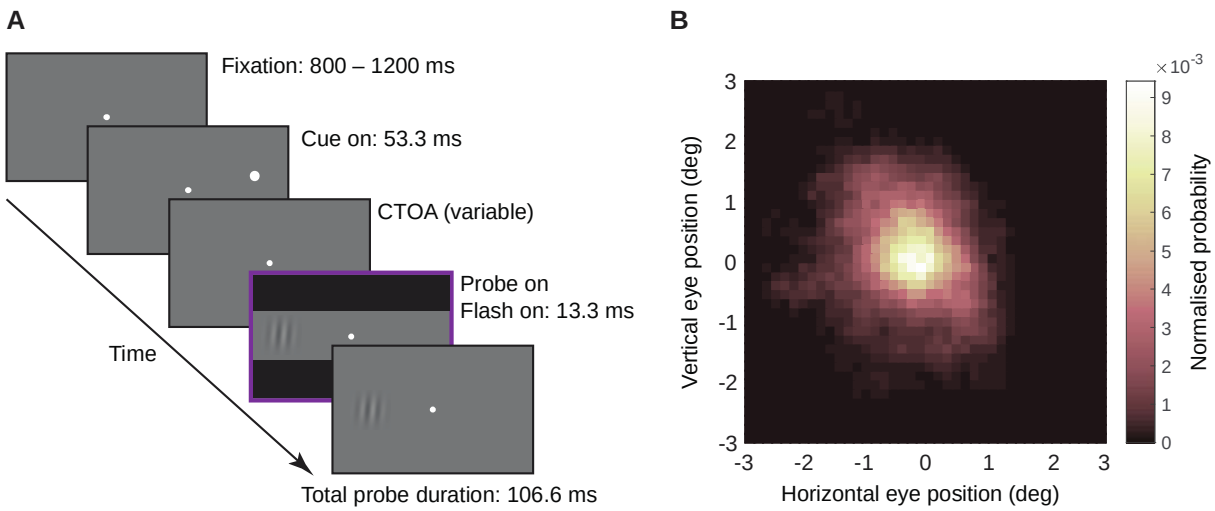

Figure 1. (A) Trial scheme. Each trial started with the onset a fixation point. After a random interval between 800 to 1200 ms, a white dot cue was presented for 53.3 ms at 10 degrees to one side of fixation. After a random interval between 120 to 306.6 ms after cue onset (CTOA), the probe was presented for 106.6 ms either at the same (congruent) or the opposite (incongruent) location as the cue. On half of the trials, a flash appeared with the onset of the probe covering the bottom and top thirds of the screen for 13.3 ms. Here we show the example of an incongruent plus flash trial. Stimuli are not drawn to scale. **(B)** Raw eye movement positions across all subjects during the period of stable fixation between 200 ms before cue onset to 200 ms after probe onset. The fixation interval spanned from a minimum duration of 515 ms and maximum of 715 ms, depending upon the CTOA. From the figure it is clear that participants were accurately maintaining stable fixation at the centre of the screen (light colours centred around zero in both the vertical and horizontal axis).

Data processing and analysis

We collected a total of 17024 trials across all included participants. Eye movement flagging was performed in a semi-automatic fashion, with the supervision of an experienced researcher (AB). Eye movements, saccades and microsaccades, were detected automatically based on velocity and acceleration thresholds of 15 deg/s and 450 deg/s^2 respectively, then all trials were manually inspected and adjusted. Samples in which the eye signal was unstable or lost were flagged as “bad data”, and any trial containing bad samples was excluded (13%). From the total of trials with good eye movement signals, we further excluded trials in which participants responded with manual

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reaction times less than 200 ms (4.4%) or more that 3.5 standard deviation above their average response latency across the entire experiment (1.2%), leaving a total of 16044 good trials. To remove possible confounds in our results due to microsaccades (e.g. Hafed 2013), we also removed all trials with microsaccades detected between 200 ms before cue onset and 200 ms after probe onset (1633 trials removed, 10.17% of the good trials). This defined an interval of stable fixation of minimum duration 515 ms and maximum duration 715 ms, depending upon the CTOA (Fig. 1B). For the remaining trials (N = 14411), incorrect responses were coded as 0 and correct responses as 1. We then used a mixed-effects logistic regression to test the influence of cue (congruent, incongruent), flash (no flash, flash), and CTOA (four bins centred on 140, 190, 240, 290 ms) on perceptual performance.

All data pre-processing and statistical analyses were conducted with custom scripts in MATLAB R2019a (MathWorks, Inc.). The entire dataset after trial exclusion is uploaded in the Open Science Framework archive at the following link:
https://osf.io/9fnh4/?view_only=14b0ae67d49c4c1aa4898f66f20b473b

Results

The present experiment follows up the recent findings in which we reported that inducing saccadic inhibition during oculomotor programming in a variant of a double-step paradigm (Becker and Jürgens 1979) could facilitate saccade reorienting behaviour (Buonocore et al. 2017b). Based on the findings for overt saccade responses, we asked if covert orienting, that we conceptualize in the framework of premotor preparation (Rizzolatti et al. 1987; Sheliga et al. 1994; Sheliga et al. 1995), could be subjected to similar inhibitory processes triggered by flash onset and which repercussion such “covert inhibition” would have on perceptual judgements. Our hypothesis is that flash onset might hinder covert

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orienting capabilities in a specific time window, similar to how the sudden presentation of a visual stimulus can reset saccade programming about 90 ms later (Buonocore and McIntosh 2008; Reingold and Stampe 1999; Reingold and Stampe 2002). To test this hypothesis, we ran a mixed-effects logistic regression to investigate how perceptual response accuracy (0,1) was modulated by *Cue* type (congruent, incongruent), *Flash* (no flash, flash), *CTOA* (140 ms, 190 ms, 240 ms, 290 ms, representing bin center) and by the interaction between *Flash* and *CTOA*. It was not possible to include the full set of interactions because it would lead the model to fail to converge. The model is summarized in Equation 1 in Wilkinson notation (Wilkinson and Rogers 1973):

$$\text{Eq. 1: } Response = Cue + Flash * CTOA + (1 \mid Subjects)$$

As expected, we found a strong main effect of *Cue* (β = -0.165, 95% CI = [-0.243, -0.087], t = -4.150, $p = 3.338*10^{-5}$) confirming better orientation discrimination for congruently cued than for incongruently cued probes (Cameron et al. 2002). Overall, the cueing effect corresponded to an increase of about 3.5% in discrimination performance when cue location matched the following probe location. For clarity, in Figure 2A we show the mean accuracy for each condition across all CTOAs. From the figure it is clear that on average the congruent cue conditions (green and blue lines) produced better orientation discrimination that the incongruent cue condition (yellow and purple lines). The analysis also revealed an interaction between *Flash* and *CTOA* such that perceptual performance was disrupted in flash trials (Fig. 2A, blue and purple lines) compared to no flash ones (Fig. 2A, green and yellow lines), when the cue preceded the probe with a delay of 190 ms (β = -0.286, 95% CI = [-0.499, -0.074], t = -2.643, p = 0.008) and 240 ms (β = -0.269, 95% CI = [-0.498, -0.040], t = -2.305, p = 0.021). Figure 2B illustrates this interaction, plotting

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the difference between flash and no flash trials (irrespective of cue). Perceptual discrimination in the middle bins of the CTOA range was reduced by about 4%.

The trend for each condition across time in Figure 2A suggests that the effect of the flash may be mostly driven by the incongruent cue condition (yellow line), rather than the congruent cue condition (blue line). We explored this pattern by running two separate mixed-effects logistic regressions to test the influence of Flash and CTOA, and their interaction, on the congruent and incongruent trials. There were no significant effects for the congruent cue condition, including in the interaction term at any of the CTOAs, while there was an interaction in the incongruent cue condition with a strong effect of the flash at 190 ms (β = -0.348, 95% CI = [-0.646, -0.050], t = -2.292, p = 0.022) and 240 ms (β = -0.393, 95% CI = [-0.716, -0.071], t = -2.389, p = 0.017). While this analysis does not formally establish a three-way interaction, it is consistent with a stronger inhibitory influence of the flash in incongruent trials, specific to the two middle time bins (190, 240 ms).

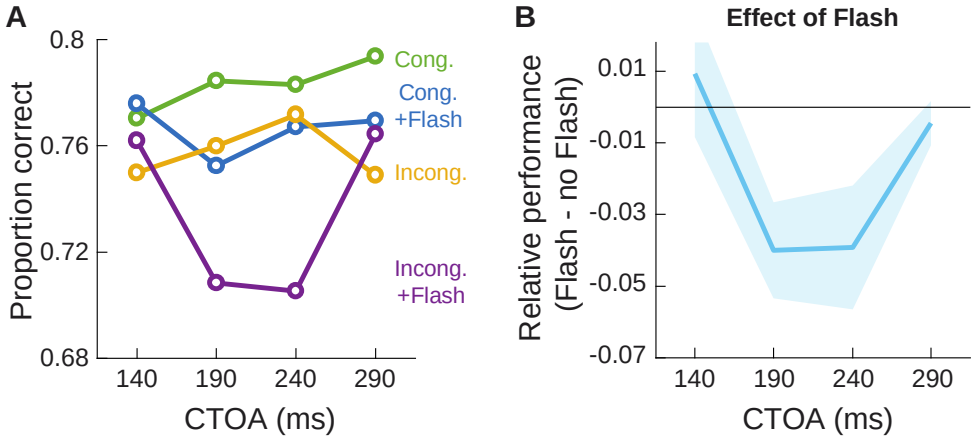

Figure 2. (A) Perceptual performance. Congruent cues (green and blue lines) lead to better performance than incongruent cues (yellow and purple lines). Flash onset (blue and purple lines) interfered with orienting behaviour reducing accuracy relative to trials in which the flash was absent (green and yellow lines respectively). The effect was more pronounced when the cue was presented 190 to 240 ms before probe onset and for the incongruent condition (purple line). **(B)** Relative effect of the flash calculated as accuracy for flash trials minus no flash trials. A clear decrease in perceptual discrimination is visible for the middle range CTOAs. Shaded areas represent one standard error of the mean.

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This pattern is clearly evident in Figure 3, where we show the raw data points of our individual participants, contrasting the no flash against flash condition at each CTOA for both the congruent (Fig.3A, top row panels) and the incongruent (Fig.3B, bottom row panels) cue condition separately. The figure clarifies that perceptual performance in the congruent cue condition was at most only lightly affected by the flash (decrease in performance observed in 8 out of 14 participants), in the two middle CTOA bins (190, 240 ms). On the other hand, in the incongruent cue condition at the mid CTOAs such shift was stronger (decrease in performance observed in 11 and 12 out of 14 participants respectively).

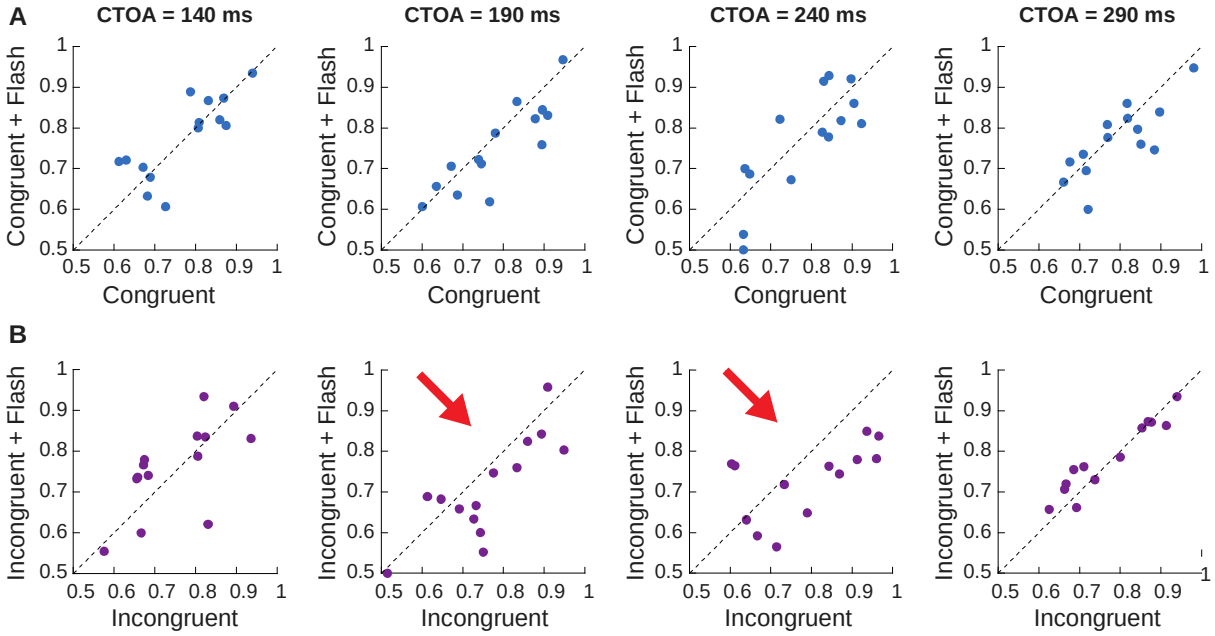

Figure 3. Raw data points of individual participants contrasting the no flash condition against flash condition at each CTOA for the congruent **(A)** and incongruent **(B)** cue condition. Dotted lines represents the unity slope line. At CTOA 190, there is a weak decrease in performance in the congruent cue condition when the flash was present. Such decrease was much stronger and sustained in the incongruent cue condition at both CTOAs of 190 ms and 240 ms (red arrow). Early and late CTOAs did not show any difference for trials with or without flash.

Discussion

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In the present manuscript, we uncovered a new phenomenon within a classic cueing paradigm (Cameron et al. 2002; Posner 1980) in which the visual discrimination for a probe stimulus was deteriorated by the simultaneous presentation of a brief flash event, but only when the flash was preceded by the exogenous cue between 165 to 265 ms. The effect was particularly emphasised for the condition in which cue location was incongruent with the location of the incoming probe. We suggest that the buildup of attentional resources at a cue location has a specific temporal window in which an inhibitory signal can interfere, leading to a “covert inhibition” effect. The mechanisms behind the inhibitory process might share similar characteristics with to the ones observed in the well-known phenomenon of SI for overt saccadic responses (Bompas and Sumner 2011; Buonocore and McIntosh 2008; Buonocore and McIntosh 2012; Edelman and Xu 2009; Reingold and Stampe 1999; Reingold and Stampe 2002) in which the flash stops the premotor buildup activity of Superior Colliculus neurons for a saccadic eye movement (Dorris et al. 2007) probably after reactivation of neurons gating saccades within the low brainstem oculomotor nuclei (Omnipause neurons, Büttner-Ennever et al. 1988; Keller 1974) (Buonocore et al. 2020; Buonocore et al. 2017a), but only within a tight temporal window before movement execution. However, the exact time course and which aspects of the covert orienting process are subjected to interference requires further investigation.

Based on the general SI framework (Reingold and Stampe 2002) and our previous findings on saccades (Buonocore et al. 2017b), we expected flash onset to interfere with covert orienting behaviour in a specific time window, inducing an SI-like inhibition effect. Beyond this, if the pattern of covert orienting was strictly following that of overt orienting as observed in our previous study, we would have expected this interruption to improve the ability to re-orient to the opposite (uncued) location, giving a relative enhancement of perceptual discrimination for incongruently cued targets. In this respect, the effect would have been the perceptual counterpart to the higher rate of successful reorienting saccades

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observed when SI was boosted in "flash-jump" trials in the overt task. The other prediction was that perceptual performance at congruent cue locations might have been slightly impaired.

Although our results confirm that the effect of the flash was time-locked to some components of the covert shift, the direction of the effect was contrary to our initial expectation. Rather than impairing orienting behaviour (congruent condition), the flash impaired the reorienting process (incongruent condition) reducing perceptual capabilities at the uncued location. This finding can perhaps be informed by the idea that reorienting following interruption after a transient event carries a small temporal cost (see reorienting latency for Experiment 3, Table 3 in: Buonocore et al. 2017b). We suggest that in our covert paradigm the flash might have introduced a similar delay during covert orienting, requiring more time to redirect to the uncued location. Given the brevity of the probe stimulus to be discriminated (106 ms), this small delay may have been enough to reduce resources at the probe location and consequently deteriorate sensitivity for the probe stimulus (Salinas and Stanford 2018). That is, while orienting (to the cued location) in our design might have been mostly or wholly completed within 100 ms, and so invulnerable to interruption by a flash, reorienting (in incongruent trials) occurred later, and was vulnerable to interruption, reducing the opportunity to process the brief probe stimulus.

It is important to emphasise that the interruption effect was restricted to the central CTOA times (165-265 ms), despite the fact that the flash was always simultaneous with the probe. This time-specificity rules out the possibility that passive masking mechanisms (Alpern 1952; Breitmeyer and Ogmen 2000) could account for the deterioration of probe discrimination; if masking were responsible, then the appearance of the flash simultaneous with the probe would always lead to the same impairment, across all experimental conditions. A precise answer to why the effect was specific for the mid-range CTOAs would required to investigate which specific components of the orienting process were

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affected by the flash. Unfortunately, the current data can not answer this point, since we have a limited CTOA time period that does not show the whole development of facilitation and inhibition following the cue. Nonetheless, our data provide a few hints to answer this question. Looking at Figure 2A, it safe to hypothesise that at the first CTOA both covert orienting (congruent cue condition) and reorienting (incongruent cue condition) could be successfully executed. This data point highlights that the covert shifts could quickly complete one cycle of orienting, toward the cue and back, within 165 ms. A similar observation can be made by looking at the microsaccade triggered after cue onset (Fig. S1A) which are a strong biomarker of covert attentional allocation (Engbert and Kliegl 2003; Hafed 2013). Again, within 150 ms, microsaccades would orient toward the cue and back, with their direction biased towards the cue (Fig. S1B) (Hafed and Ignashchenkova 2013; Malevich et al. 2020; Tian et al. 2016).

These data suggest that covert shifts following cue onset were moving with a certain periodicity, that we can estimate from our data to be about 150 ms. In support of this observation, recent theories of attentional allocation suggest that orienting is not a monotonic process but rather a dynamic sampling of spatial locations started by the onset of a lateralised stimulus with a periodicity between 200 to 250 ms depending on the experimental design (Bellet et al. 2017; Helfrich et al. 2018; Landau and Fries 2012; Song et al. 2014; VanRullen et al. 2007). We suggest that the inhibitory process we recorded may reflect interference in a specific phase of this rhythmic process between spatial locations, with the first sensitive time being after the first cycle of sampling, that in our paradigm would be at around 220 ms. Earlier time points at ~70 ms as well as later time points ~360 ms would be also expected to be suitable for interference. We recognise that the rhythmicity was hidden in our no flash conditions probably because of the mild cueing effect of our paradigm (but see Fig. S2 for a higher temporal resolution of the effect).

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Taking together these observations, we can draw some predictions from our data to apply to future research work on “covert inhibition” effects. One main hypothesis is that the flash would always alter perceptual performance when it is time-locked to the ongoing covert process triggered by the cue. The time-locking point could be determined by estimating the time at which the covert shift would engage or disengage from the cue. This point in time can be inferred by looking at how microsaccades are attracted by the cue as well as the full time course of facilitation and inhibition in no flash trials. A corollary of this hypothesis is that the time interval between cue onset and probe onset should be irrelevant to observe “covert inhibition” effects, that should always manifest as far as the flash can intercept the timing of the covert shift. This mechanisms is in fact similar to the time-locked interference of the flash relative to saccadic reaction times. Finally, the interference is expected to affect both congruent and incongruent orienting processes, but the magnitude of the effect might be modulated by the more general cueing effect. Covert inhibition effects are then expected to also extend to paradigms in which presaccadic shift of attentions are involved, altering the strong benefits of coupling covert orienting with eye movements.

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Supplementary material

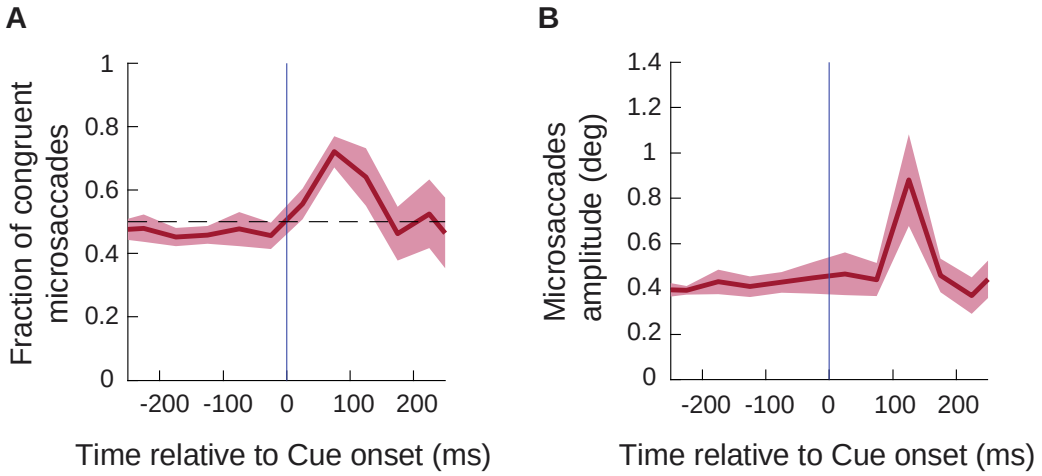

Figure S1. For each participant, we calculated the fraction of microsaccades going toward the cue **(A)**, and their average amplitude **(B)** for all the conditions pooled together. **(A)** Shortly following cue onset, microsaccades were directed toward cue location and return to baseline level about 150 ms afterward. Since in half of the trials the cue was presented at the opposite location of the probe (incongruent cue condition), this pattern suggests that eye movements were biased away from the location where the perceptual judgment would take place. **(B)** Microsaccades directed toward the cue showed an approximate doubling in amplitude. In all panels, the thick line represents the average across participants and the shaded area represents one standard error of the mean.

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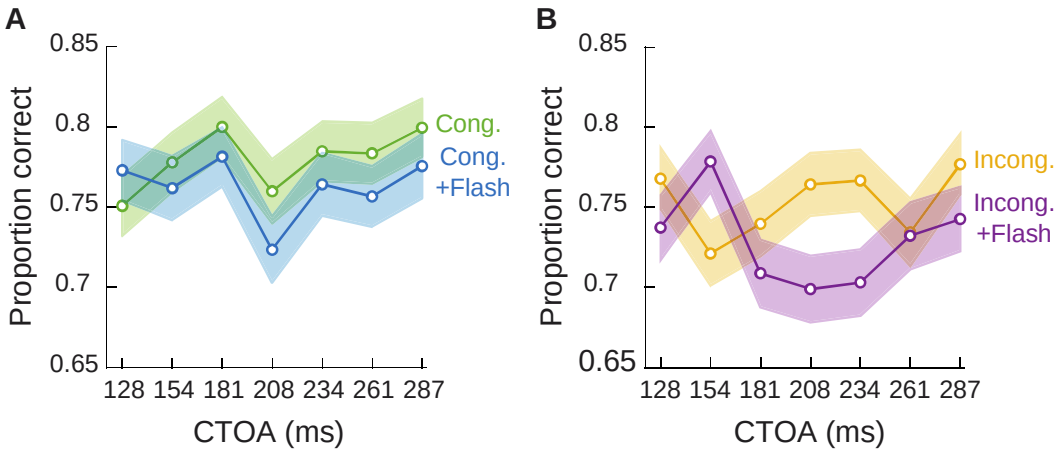

Figure S2. Time course of congruent **(A)** and incongruent **(B)** cue conditions at high temporal resolution. **(A)** As already showed in Fig. 2A, there is no clear difference between flash (blue) and no flash (green) trials in the congruent cue condition. The only indication of a stronger interference is when the CTOA is 208 ms, with performance recovering soon after. **(B)** A more clear rhythm pattern in the incongruent cue condition (yellow) emerges with higher CTOA sampling, suggesting that the probe was biasing attentional allocation. When the flash is present (purple), discrimination performance is altered following an almost antiphase pattern. Data are pooled together across participants to increase the confidence in the mean estimate. In all panels, the shaded area represents one standard error of the mean.