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RESEARCH ARTICLE | *Sensory Processing*

Discriminating between anticipatory and visually triggered saccades: measuring minimal visual saccadic response time using luminance

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Heeman J, Van der Stigchel S, Munoz DP, Theeuwes J. Discriminating between anticipatory and visually triggered saccades: measuring minimal visual saccadic response time using luminance. *J Neurophysiol* 121: 2101–2111, 2019. First published February 20, 2019; doi:10.1152/jn.00378.2018.—We describe a novel behavioral method to accurately discriminate anticipatory (i.e., saccades not generated by visual input) from visually triggered saccades and to identify the minimal visual saccadic reaction time (SRT). This method can be used to calculate a feasible lower bound cutoff for latencies of visually triggered saccades within a certain experimental context or participant group. We apply this method to compute the minimal visual SRT for two different saccade target luminance levels. Three main findings are presented: *1*) the minimal visual SRT for all participants was 46 ms shorter for bright targets than for dim targets, *2*) the transition from non-visually triggered to visually triggered saccades occurred abruptly, independent of target luminance, and *3*) although the absolute minimal visual SRTs varied between participants, the response pattern (response to bright targets being faster than to dim targets) was consistent across participants. These results are consistent with variability in saccadic and neural responses to luminance as has been reported in monkeys. On the basis of these results, we argue that differences in the minimal visual SRT can easily occur when stimuli vary in luminance or other saliency features. Applying an absolute cutoff (i.e., 70–90 ms) that approaches the minimal neuronal conduction delays, which is general practice in many laboratories, may result in the wrongful inclusion of saccades that are not visually triggered. It is suggested to assess the lower SRT bound for visually triggered saccades when piloting an experimental setup and before including saccades based on particular latency criteria.

NEW & NOTEWORTHY We successfully developed an anticipation paradigm to discriminate between anticipatory and visually triggered saccades by measuring the minimal visual saccadic response time (SRT). We show that the 70- to 90-ms lower bound cutoff for visually triggered saccades should be applied in a flexible way and that the transitional interval is very short. The paradigm can be employed to investigate the effects of different stimulus features, experimental conditions, and participant groups on the minimal visual SRT in humans.

anticipatory saccade; latency; luminance; visual processing time; visually triggered saccade

INTRODUCTION

Although visual processing of an object starts at the moment a new element appears in the visual field, this process takes time to develop. When an eye movement is made before sufficient visual processing has taken place, the eye movement is considered to be anticipatory and not visually triggered (Dorris and Munoz 1998). Anticipatory saccades are not generated by visual input, but instead are based on cognitive factors, such as predictions, knowledge, beliefs, expectations, predictions, or strategy, or even based on coincidence (Badler and Heinen 2006; Kalesnykas and Hallett 1987; Smit and Van Gisbergen 1989). Within the context of this study, we regard anticipatory saccades as all those saccades that are not target driven irrespective of what caused the anticipation. In contrast, saccades to abrupt visual onsets that are initiated after sufficient visual processing are predominantly visually triggered. The minimal physiological reaction time of visually triggered saccades can be defined by the sum of the delay of afferent signals reaching the core oculomotor structures (e.g., frontal eye fields, superior colliculus) and the efferent signal delays from these structures to the extraocular muscles (Carpenter 1981; Dorris et al. 1997, 2007; Edelman and Keller 1996; Fischer and Boch 1983; Fischer and Ramsperger 1984).

Many studies regard the minimal physiological visually triggered saccadic response time (minimal visual SRT) as a constant and assume it takes 70–90 ms for a visual signal to travel from the retina through the brain to the eye muscles, independent of stimulus features, laboratory conditions, or participant characteristics (Becker 1989; Currie et al. 1993; Fischer and Boch 1983; Fischer and Breitmeyer 1987; Fischer and Weber 1993). This assumption is based on neurophysiological research in monkeys that reports a minimum conduction delay of 70 ms from retina to the eye muscles (Dorris and Munoz 1998; Dorris et al. 1997; Edelman and Keller 1996; Sparks et al. 2000; Sparks 2002) and is supported by human behavioral research that shows that the fastest visually triggered responses to the appearance of a visual stimulus are not earlier than ~90 ms (Cavegn 1996; Heeman et al. 2014, 2017; Wenban-Smith and Findlay 1991). However, recently, single-cell recordings in the monkey superior colliculus (SC), a midbrain structure that is crucial for eye movement control, have shown that the arrival time and magnitude of the visual response in the SC and the subsequent SRT are significantly

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modulated by target luminance (Bell et al. 2006; Li and Basso 2008; Marino et al. 2012b, 2015; Marino and Munoz 2009). It was shown that the SRTs decreased with increasing target luminance. Accordingly, many behavioral studies have shown that SRT is influenced by various external factors (see Sumner 2011 for a review) including stimulus features (Boch et al. 1984; Marino et al. 2015; e.g., Bompas and Sumner 2008, 2009; Carpenter 2004; Doma and Hallett 1988; Marino et al. 2012a; Wheeless et al. 1967), experimental design (e.g., Carpenter and Williams 1995; Dorris and Munoz 1995, 1998; Fischer and Ramsperger 1984; Heeman et al. 2017; Kalesnykas and Hallett 1994), and task requirements (e.g., Bucker et al. 2015; Rothkirch et al. 2013; Walker et al. 2000). In addition, age (Carter et al. 1983; Irving et al. 2006; Kramer et al. 1999; Munoz et al. 1998; Peltsch et al. 2011), diseases such as Parkinson's (Chan et al. 2005), Huntington's (Blekher et al. 2006), and Alzheimer's (Yang et al. 2011) and even general fluid intelligence (Haishi et al. 2011) can impact SRT. In light of these findings it seems questionable whether the minimal visual SRT should be considered to be a constant value.

It is generally believed that it is important to make a distinction between visually triggered and anticipatory saccades, because the erroneous inclusion of anticipatory saccades in data analysis can significantly alter the conclusions of a study with regard to, for instance, response times to visual input. Also, showing a difference between anticipatory and visually triggered saccades is important in the detection of express saccades (defined as the earliest visually triggered saccades). It is often stated that express saccades occur only between ~70 and ~130 ms (Dorris et al. 1997; Fischer and Boch 1983; Fischer and Ramsperger 1984; Fischer and Weber 1993; Paré and Munoz 1996) or can be detected on the basis of bimodal latency distribution (Fischer and Boch 1983; Heeman et al. 2017; Fischer et al. 1984). If, however, the minimal visual SRT is context dependent, express saccade production may not be limited to the specified latency window but may very well occur later in time. This shift in time would merge their latency distribution with regular latency saccades. Therefore, before a new experiment involving measures of SRT is started, there may be a need to determine the human minimal visual SRT within a given context. In the current study, we present a method to accurately measure the experiment-specific minimal processing time required to translate a visual signal into a saccade.

The different response characteristics of anticipatory and visually triggered saccades (i.e., anticipatory: in any direction; visually triggered: in the target direction) provide the basic idea behind the hypothesis that we present in this article. All relevant stimuli in the visual field produce a transient peak of activation in the retinotopic SC map (Marino et al. 2008; Munoz and Wurtz 1995a; Munoz and Wurtz 1995b; White et al. 2017). When the subsequent stimulus-related activity at one specific location in the SC (priority) map surpasses the saccade trigger threshold (Godijn and Theeuwes 2002; Hanes and Schall 1996; Meeter et al. 2010; Paré and Hanes 2003; Trappenberg et al. 2001), a visually triggered saccade is, unavoidably, made in the direction of that location (Lee et al. 1991; Sparks and Mays 1980; White et al. 2017). In contrast, when a saccade is initiated before visual input drives the SC activity past the response threshold, any location in the visual field, depending on the intentions of the participant, is capable of being the saccade goal and will result in an anticipatory saccade. We hypothesize that by measuring the accuracy of the direction of the saccade, we can measure at what time point the visually driven activation has surpassed the response threshold and thus determine the minimal visual SRT.

In a simple gap task, we instruct participants to make an eye movement to one of two possible target locations (left or right) in response to an auditory GO signal. The temporal gap before the target appearance facilitates the production of low-latency saccades because it allows disengagement from one object before a saccade is initiated to the next object (Heeman et al. 2017; Dorris and Munoz 1995; Saslow 1967; Reuter-Lorenz et al. 1991). The GO signal (duration 100 ms), however, is delivered before the start of the temporal gap between fixation offset and target appearance and ends 200 ms before the appearance of the visual target. Due to the temporal gap between fixation offset and target appearance, and the auditory GO signal, participants are stimulated to respond fast and to make both anticipatory and visually triggered saccades. The naturally occurring variability in SRTs should warrant that the data contains a substantial number of anticipatory and visually triggered saccades. We predict that anticipatory saccades will have a 50% chance of going to the correct, out of two, target location, whereas visually triggered saccades will almost exclusively be directed toward the target. Based on the results of previous SC recording studies in monkeys, the transitional interval from anticipatory to visually triggered saccades will be revealed by a rapid decrease in the number of saccades to the incorrect target location once visual processing has been sufficient to cross the response threshold (e.g., Dorris et al. 2007). The point in time where this steep drop in incorrect saccades occurs is considered the minimal visual SRT.

Because it has previously been shown that the luminance of the target affects visual SRTs (Doma and Hallett 1988; Wheeless et al. 1967), we choose this feature to test our hypotheses and to make a cross-species comparison between monkeys and humans. In the current study, we specifically built on previous behavioral neurophysiological results obtained from monkey superior colliculus recordings (Marino et al. 2012a, 2015). In these previous experiments in monkeys, seven luminance levels were used while saccadic reaction times and single-neuron activity in the superior colliculus were recorded simultanously. We choose two luminance levels to match two extreme values used by Marino et al. (2015): a high luminance level (42.5 cd/m^2) and a lower luminance level (0.33 cd/m^2), where SRT was still correlated with visual response onset latencies in the monkey SC (above 0.044 cd/m^2; see Fig. 5). By measuring many trials for these two luminance levels, we can make an accurate estimate of the minimal visual SRT, which is defined as the earliest time point at which the correct responses start to rise to maximum and the incorrect responses drop to a minimum. This allows us to make a cross-species comparison between monkeys and humans and to demonstrate that luminance changes of the target impact visually triggered SRTs in humans in a systematic manner, similar to what has been shown in monkeys.

MATERIALS AND METHODS

Participants

This study included 22 participants (age: 19–24 yr, mean = 23.6 yr; 14 women, 8 men; 18 Caucasian). All participants self-reported that they had normal or corrected-to-normal (i.e., glasses or contacts)

visual acuity. Participants were compensated $20 CAD per hour for participating. This study was approved by the Queen's University Human Research Ethics Board and was in accordance with the Canadian Tri-council Policy Statement on Ethical Conduct for Research Involving Humans and the Code of Ethics of the World Medical Association (Declaration of Helsinki) for experiments involving humans. All participants gave written informed consent and were compensated for their time.

Apparatus

The experiment was performed in a sound-attenuated, dimly lit room. Participants viewed an LCD monitor (1,280 × 1,024 pixels, 75 Hz; model no. AL1717; Acer) at a distance of 60 cm. The overall system lag, defined as the time difference between giving the command to send the display to the monitor (synchronized to the refresh rate of the monitor) and the appearance of the display on the monitor, was measured using a photo diode [mean 13.28 ms (SD 0.358)]. Eye movements were recorded monocularly with an EyeLink 1000 video-based eye tracker with a temporal resolution of 1,000 Hz and a spatial resolution of 0.01° (desktop system; SR Research). A chin rest stabilized the participants' head and helped participants maintain a fixed viewing distance.

Stimuli and Procedure

Before the experiment was started, the eye tracker system was calibrated by sequentially fixating a known grid of nine target points. During the subsequent validation routine, the calibration accuracy, i.e., the distance between the eye position and the target point, was assessed as validation error and expressed in degrees of visual angle from the target point. Calibration was only accepted when none of the validation errors was larger than 1° visual angle. The eye that gave the highest accuracy (i.e., lowest average error) was recorded (for 13 participants, the right eye was recorded; for 9 participants, the left eye was recorded). Each experimental session started with 12 training trials in which the participant was instructed on the task.

Each trial started by fixating a dot on the center of the screen. After 50 ms of fixation, the dot was replaced with a white fixation cross (1.1° × 1.1° visual angle, 92.6 cd/m^2) on a black background (0.20 cd/m^2). The fixation cross was displayed for 1,000 ms, and during the last 100 ms an acoustic GO signal (2,000 Hz for 100 ms) was given. Simultaneously with the offset of the GO signal, the fixation cross was removed from the screen, leaving a gap of 200 ms before the target appeared. The target was a high-luminance or low-luminance gray filled circle (1.1° visual angle) presented at an eccentricity of 10° visual angle on either the left or the right side of the location of the central fixation cross. The respective luminance levels were specifically chosen to match two values used by Marino et al. (2015): a high-luminance level (bright: 42.5 cd/m^2) and a lower luminance level (dim: 0.33 cd/m^2) where SRT was still correlated with visual response onset latencies in the monkey SC (above 0.044 cd/m^2). The target was removed after 1,200 ms, after which the next trial started. See Fig. 1 for a schematic of the timing and trial sequence.

Participants' instructions were critical because the analysis relied on inclusion of both anticipatory and visually triggered saccades. Participants were specifically instructed to make one eye movement to the target as soon as they heard the GO signal. It was explained that there were two possible target locations and that the eye movement should always go to one of the two possible locations. Participants were instructed not to predetermine the direction they would move their eyes in. Participants were also instructed to make a corrective saccade to the target in cases when they made the saccade to the wrong side to ensure they were paying attention to the target. Speed was more important than accuracy. The timing of the stimulus presentation and the natural distribution of the participants' reaction times ensured that some eye movements were initiated before target appearance, whereas others were not made until after target appearance.

The experiment consisted of a single session of 576 trials divided into 18 blocks of 32 trials. Between the blocks, participants could take a break and decide when to continue to the next block. Halfway through the experiment, participants got a longer break to renew their alertness, followed by recalibration of the eye tracker. Each of the two experimental conditions (bright and dim target) was presented 288 times with an equal number of presentations on the left and right sides of the screen. The conditions were intermixed, counterbalanced (equal number of trials per condition per block), and randomized across the experiment.

Data Analysis

Preprocessing and exclusion criteria. Saccades were defined as eye movements with an eye velocity that exceed 35°/s or eye acceleration that exceeded 9500°/s^2. SRT was defined as the time from target appearance to the initiation of the first saccade. Negative SRT values meant that a saccade was made before the appearance of the target (i.e., anticipatory saccades). Saccades that were initiated before the removal of the fixation cross (200 ms before target appearance) were excluded from the analysis because these saccades were initiated before all information (GO signal, removal of fixation) that was needed to comply with the instructions was presented. Saccades with an SRT over 500 ms were excluded from the analysis because they were considered to be too slow to be of interest for this study. Saccade amplitude was defined as the distance between the starting point of the saccade and the saccade end point, in degrees of visual angle. Before analysis, trials were visually inspected and filtered, and were excluded if they contained technical errors, blinks, or if the duration of the first saccade exceeded 75 ms. Eye movements that started before the end of the GO signal were excluded from the analysis. To be included in the analysis, the saccade had to have a minimal amplitude of 2° visual angle and had to have started within 2° of the center of the fixation cross. Saccades initiated in the direction of the target location were

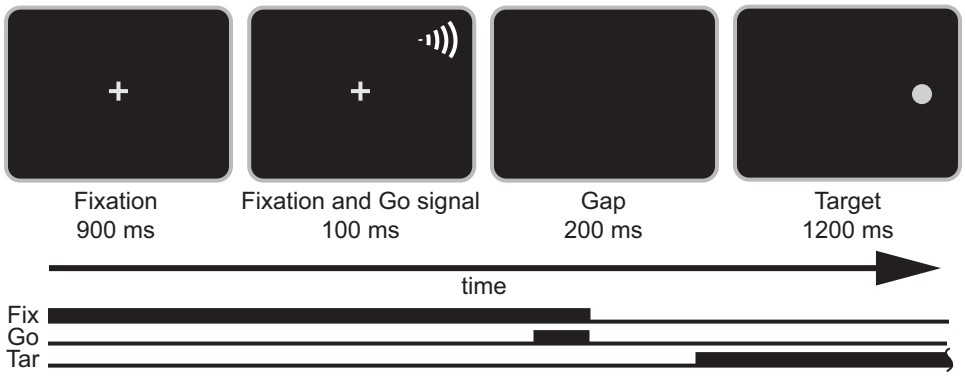

Fig. 1. Schematic of the trial sequence and timing. Task instruction: "Make one eye movement to the target as soon as you hear the GO signal; mistakes are okay as long as you correct the eye movements as soon as you notice your mistake." Tar, target.

classified as correct; saccades initiated in the opposite direction of the target location were classified as incorrect.

Statistical analysis. Within the context of this study, anticipatory saccades are considered all saccades that were not target driven and that occurred before the minimal physiological latency, independent of what might have caused the anticipation. Visually triggered saccades are all saccade made in response to the appearance of the visual target. To determine at what time point after target appearance the transition from anticipatory to visually triggered saccades occurred, we tested at what SRT the proportion of saccades to the target (correct saccades) was larger than the percentage of saccades to the opposite side of the target (incorrect saccades). Trials were split according to luminance level (bright and dim), sorted according to SRT (low to high), and binned in 10-ms bins containing the number of correct and incorrect saccades in each bin. For both luminance levels, a one-sided Wilcoxon signed-rank test for nonparametric data was used to determine, for each luminance level, the SRT bin for which the number of correct saccades was significantly larger than the number of incorrect saccades. This SRT is the minimal SRT for which the saccades were visually triggered (minimal visual SRT). Because the transition from anticipatory to visually triggered saccades can only occur after target presentation and is unlikely to occur once the target has been visible for more than 250 ms (Heeman et al. 2017), only saccades with a SRT between 55 and 250 ms after target appearance were included in the analysis.

The approach to determine the minimal visual SRT as described above, where we assess the statistical difference between number of correct and incorrect responses, results in slightly elevated values for the minimal visual SRT because this difference needs time to accumulate before it reaches a statistically significance level. Based on our assumption that upon sufficient visual processing the number of incorrect responses quickly drops to zero, the minimal visual SRT would shift toward a "kink" in the distribution provided there was an extremely large number of samples. Therefore, we applied a second, qualitative method to determine the minimal visual SRT. This method entailed plotting the cumulative distribution of all SRTs per participant and assessing at what SRT the increase of incorrect saccades stopped and the number of correct and incorrect saccades started to diverge. This point of divergence can be referred to as the kink in the cumulative distribution and provides a second method to estimate the minimal visual SRT. The minimal visual SRT for the two luminance levels and the two methods for determining the minimal visual SRT were compared by using a repeated-measures analysis of variance (ANOVA) with luminance (bright and dim) and method (statistical and kink) as factors. To assess the generalizability of the results for minimal visual SRT between monkeys and humans, we directly compared the monkeys' minimal visual SRT as previously published (Marino et al. 2015) and the human minimal visual SRTs based on the data collected in the current study.

In addition, to determine whether "fast" participants were fast in both the bright and dim target conditions, the within-participant Pearson correlation between the minimal visual SRT for bright targets and the minimal visual SRT for dim targets was calculated. Also, the rise of the number of correct response was analyzed by calculating the slope of an interval of 20 ms around minimal visual SRT (the transitional interval) for each participant and each condition. The average slopes for both conditions (bright and dim) were compared using a paired-sample *t*-test.

Finally, we explored the amplitude and main sequence (peak velocity as a function of amplitude) (Bahill et al. 1975) of the saccades by selecting a subset of participants that produced similar numbers of anticipatory and visually triggered saccades in both conditions (bright and dim). The minimal visual SRT distinguishing anticipatory from visually triggered saccades was based on the kink in the individual distributions. A repeated-measures ANOVA with saccade category (anticipatory and visually triggered) and luminance (bright and dim) as factors was used to test the main effects of category and luminance and their interaction with amplitude. Because of the known linear relationship between saccade amplitude and peak velocity (Bahill et al. 1975), we restricted saccade amplitude to 8.3°–9.3° for the peak velocity analysis. This amplitude range was restricted, yet contained enough saccades of all types (i.e., anticipatory, visually triggered, correct, and incorrect) to conduct the analysis. A repeated-measures ANOVA with saccade category (anticipatory and visually triggered) and luminance (bright and dim) as factors was used to test the main effects of category and luminance and their interaction with peak velocity. Holm-Bonferroni correction was applied to compensate for multiple comparisons.

RESULTS

Exclusions

Based on the exclusion criteria (see MATERIALS AND METHODS), an average of 11.0% (SD 6.2) of the trials were excluded from the analysis. The primary reason for exclusion of trials was that saccades were made before the removal of the fixation cross [i.e., before the end of the GO signal: 5.7% (SD 3.2)]. The remaining 5.3% of the excluded trials were mainly due to eye blinks.

Saccade Response Time

Figures 2 and 3 show the mean (Fig. 2) and individual (Fig. 3) SRT distributions for all 22 participants for trials that were initiated in the direction of the target (correct saccades) and trials that were initiated in the opposite direction of the target (incorrect saccades) for both the bright and the dim target conditions. The first important point is that the distributions are shifted dramatically in time from target appearance for the two luminance conditions. The second important point is that the correct and incorrect direction distributions are identical until a certain point after target appearance. Of 22 participants, depending on the method used, 17 or 16 participants produced enough correct and incorrect saccades to calculate the individual minimal visual SRT using the statistical approach or the kink method, respectively, as depicted in Fig. 3. The Wilcoxon signed-rank test showed that the first significant difference between percentage of correct and incorrect saccades for bright targets occurred at 97 ms (SD 10; $W = 48$, $Z = 3.155$, $P = 0.002$, $r = 0.74$; Fig. 2*A* and Fig. 3, individual *top* plots). This means that up to 97 ms after stimulus appearance, the chance of making a saccade to the target or making a saccade to the opposite side of the target was equally likely. From 97 ms onward, the number of correct saccades to the target increased dramatically, while the number of incorrect saccades almost simultaneously dropped to 0. For the dim stimulus, the transition from chance-level (0.5) performance to mainly correct saccades to the target occurred at 143 ms (SD 22.6; $W = 60$, $Z = 2.511$, $P = 0.012$, $r = 0.61$), indicating that up to 143 ms after target appearance, performance was at chance level. When the minimal visual SRT was determined by assessing the kink in the cumulative distribution (Fig. 2*B* and Fig. 3, individual *bottom* plots). Visually triggered saccades to the bright target had a minimal visual SRT of 88 ms (SD 9.6), and visually triggered saccades to a dim target had a minimal visual SRT of 131 ms (SD 8.9). Comparison of the minimal visual SRTs for the two luminance levels shows there was a main effect of luminance [$F(1,15) = 224.8$, $P < 0.001$, $\eta_p^2 = 0.937$], showing that bright targets elicited a shorter minimal visual SRT than dim targets. Also, there was a main effect of method [$F(1,15) = 8.682$, $P = 0.010$, $\eta_p^2 = 0.367$], showing that, overall, the minimal visual SRTs as determined using statistical comparisons were longer

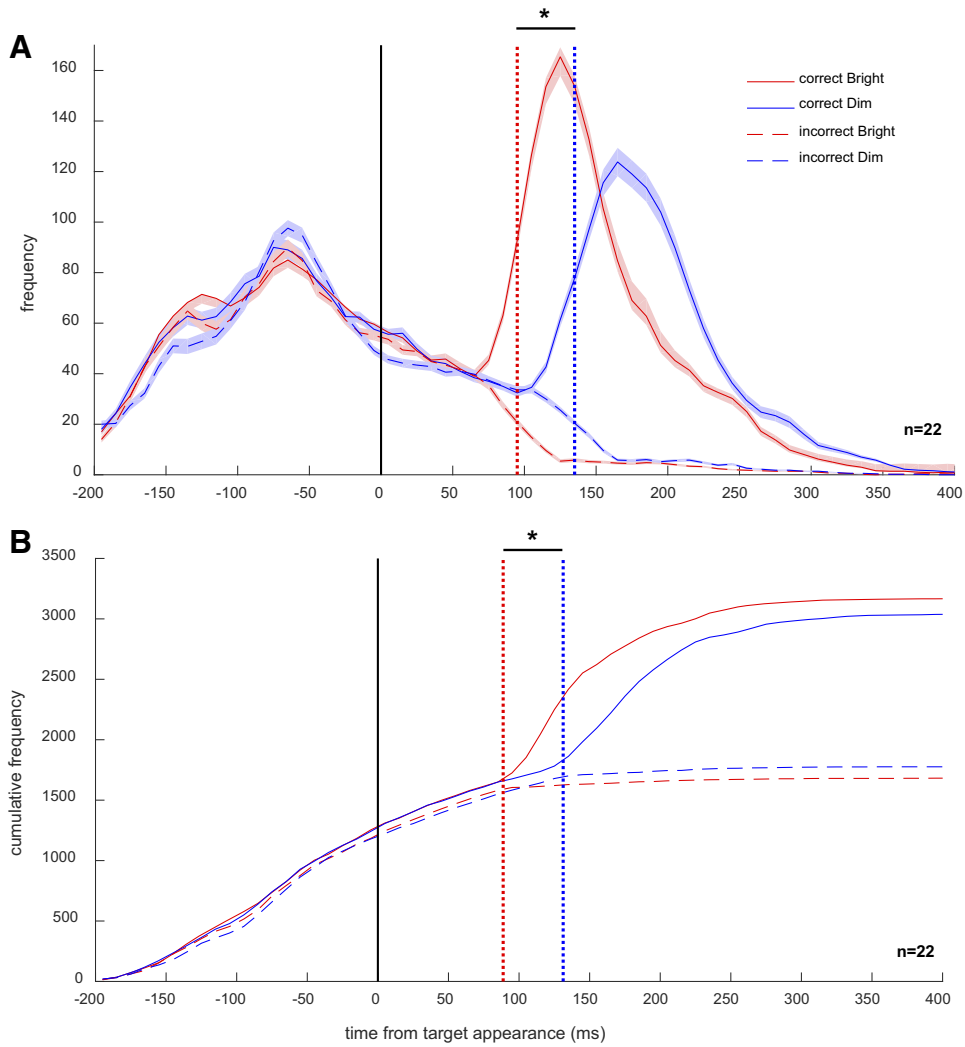

Fig. 2. *A*: overall saccade response time (SRT) distribution for all 22 participants of correct (solid lines) and incorrect trials (dashed lines) in the bright (red) and dim (blue) target conditions. Shaded area denotes SE across participants. *B*: cumulative distribution for all 22 participants. The vertical dotted lines (red or blue) after target appearance (vertical solid line) visualize the minimal visual SRT, i.e., the boundary between anticipatory and visually triggered saccades, for each condition. *Main effect of luminance (*A* and *B*): $F(1,15) = 224.8$, $P < 0.001$, $\eta_p^2 = 0.937$.

then when that same point was determined using the kink method. However, there was no interaction [$F(1,15) = 1.378$, $P = 0.259$, $\eta_p^2 = 0.084$], which means that regardless of the method used, the minimal visual SRT to bright targets was shorter than the minimal visual SRT to dim targets.

It was not possible to calculate the minimal visual SRT and the slope of the transitional interval for all participants, as can be seen in the individual participant plots of *participants 3*, *4*, *9*, *13*, *19*, and *21* in Fig. 3*B*. Two main causes were identified: *1*) the minimal visual SRT could not be calculated when almost all of the saccades were initiated before the target appearance, as was the case for *participants 9*, *13*, *19*, and *21* (Fig. 3*B*, first 4 columns), and *2*) participants ignored the target and made a saccade based on internal cues (e.g., predetermining the saccade direction based on the previous trial), which is reflected in the random distribution of correct and incorrect saccades throughout the SRT distribution, as was the case for *participants 3* and *4* (Fig. 3*B*, last 2 columns). Although the data from *participant 13* did result in a feasible minimal visual SRT, the number of visually triggered saccades was too low to asses a kink in the cumulative distribution. Including or excluding data from these participants did not change the results, and the data from all participants are included in the analyses whenever possible.

The mean difference between the minimal visual SRT to bright and dim targets was 46 ms (SD 12). This difference was significant, as indicated by a *t*-test comparing the minimal visual SRT between the bright and dim target conditions [$t(12) = 13.182$, $P < 0.001$]. The minimal visual SRT for bright stimuli ranged between 82 and 116 ms, whereas the minimal visual SRT for dim targets ranged between 123 and 193 ms (Fig. 4*A*). There was a positive correlation (Fig. 4*B*) between the minimal visual SRT for bright targets and the minimal visual SRT for dim targets for all participants ($r = 0.729$, $n = 17$, $P < 0.001$), indicating that participants who had the shortest minimal visual SRT for saccades to bright targets also had the shortest minimal visual SRT for saccades to dim targets. Indeed, minimal visual SRTs in the bright target condition are significant predictors for minimal visual SRTs in the dim target condition [SRT bright $= -2.0497 + 1.4894 \times$ SRT dim; $F(17,15) = 15.2$, $P = 0.001$]. Also, judging from the slope of the SRT distribution, the transition from anticipatory to visually triggered saccades in both the bright and the dim target conditions occurred within a very short time span of ~10 ms. The average slopes per participant of the transition from anticipatory to visually triggered saccades for the bright [mean 0.26 (SD 0.24)] and the dim targets [mean 0.27 (SD 0.21)] showed no systematic differences [$t(42) = 0.034$, $P = 0.973$].

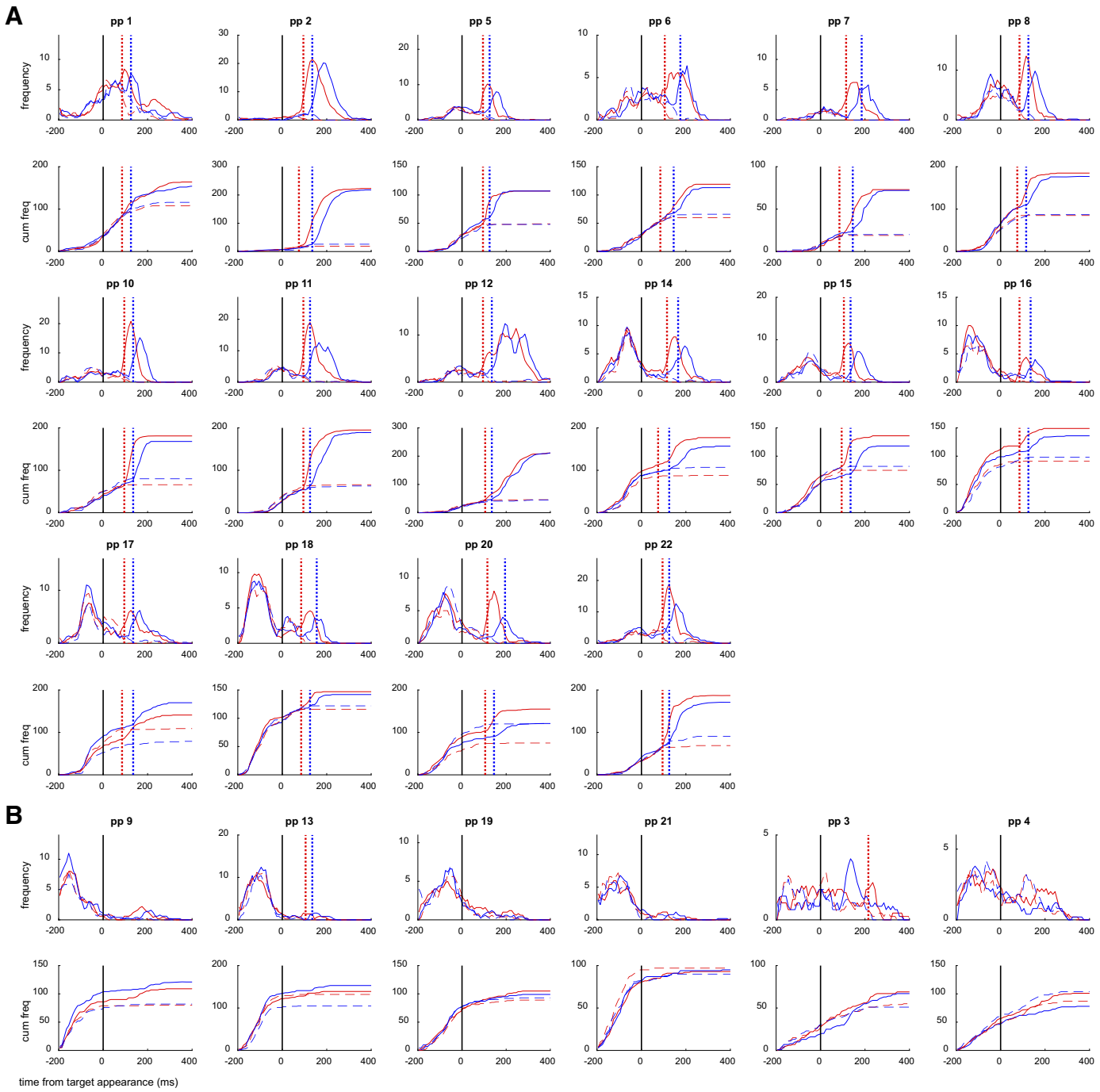

Fig. 3. *A*: saccade response time (SRT) distributions and minimal visual SRT per participant. SRT distributions (*top* plot per participant) and cumulative SRT distributions (*bottom* plot per participant) for correct (solid lines) and incorrect trials (dashed lines) in the bright (red) and dim (blue) target conditions. The vertical dotted lines (red or blue) after target appearance (vertical solid line) visualize the minimal visual SRT, i.e., the boundary between anticipatory and visually triggered saccades, for each condition. *B*: SRT distributions for participants for whom it was not possible to calculate all minimal visual SRTs. cum, Cumulative; freq, frequency; pp, participant.

Cross-Species Comparison

Figure 5 shows the relationship between human minimal visual SRT and target luminance and the relationship between monkey minimal visual SRT and target luminance (as previously published; see Marino et al. 2015). It is clear from Fig. 5 that there is a remarkable cross-species correspondence between monkey and human minimal visual SRTs as a function of luminance. Although monkeys had overall faster responses than humans (for monkey vs. human difference in minimal visual SRT, see also Fischer and Boch 1983; Fischer and Ramsperger 1984), both species show the same decrease in minimal visual SRT as a function of increasing luminance. The minimal visual SRT determined by qualitatively assessing the kink in the cumulative distribution where the number of correct and incorrect saccades start to diverge is slightly earlier than the minimal visual

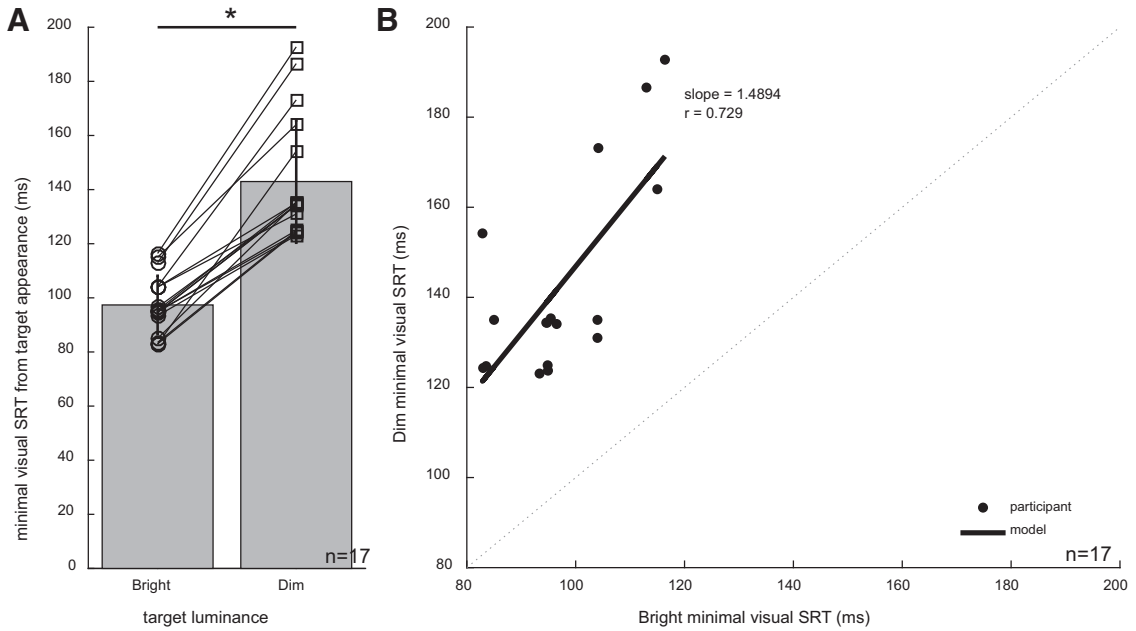

Fig. 4. *A*: the mean minimal visual saccadic response time (SRT) of the first SRT bin showing a significant difference between correct and incorrect saccades for the bright target (○) and the dim target (□) ($n = 17$ participants, 9 female). *$P < 0.001$, $t(12) = 13.182$, significant difference for bright vs. dim target. *B*: the correlation between minimal visual SRT for bright and dim targets per participant ($n = 17$, 9 female).

SRT determined on the basis of the Wilcoxon signed-rank test (see *Saccadic Response Time*). The trend for both estimates, however, is identical and shows a systematic shift in minimal visual SRT that is produced by luminance both for monkeys and humans.

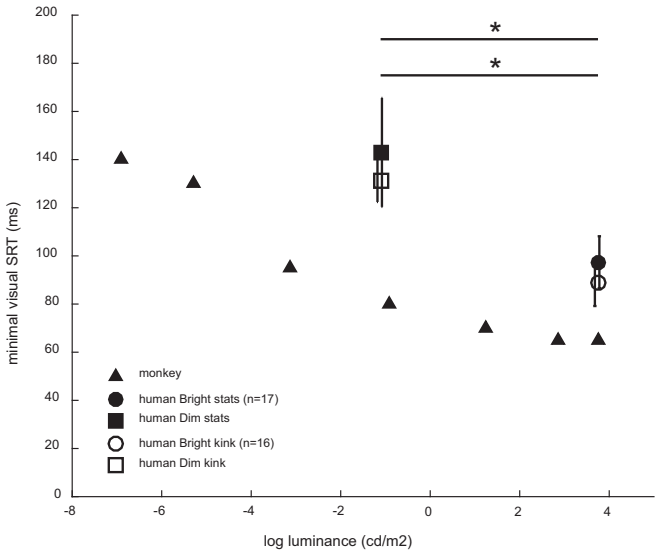

Fig. 5. Cross-species comparison of the average minimal visual saccade response time (SRT) as a function of target luminance in human participants with the previously published (Marino et al. 2015) experimental minimal visual SRT in awake monkeys (▲) for 7 luminance levels. Closed symbols represent the statistical method for determining the human minimal visual SRT (stats; $n = 17$ participants, 9 female) and open symbols depict the human minimal visual SRT when the cumulative distribution was assessed qualitatively (kink; $n = 16$ participants, 9 female) in bright (circles) and dim (squares) target conditions. *Main effect of luminance: $F(1,15) = 224.8$, $P < 0.001$, $\eta_p^2 = 0.937$.

Saccade Amplitude and Peak Velocity

When saccade amplitude is examined for all conditions, saccades show a slight undershoot, with saccades not completely reaching the target (at 10° visual angle eccentricity; Fig. 6*A*). Overall, the amplitudes of anticipatory saccades were shorter than amplitudes of visually triggered saccades [$F(1,15) = 41.073$, $P < 0.001$, $\eta_p^2 = 0.732$]. There was, however, no main effect of luminance [$F(1,15) = 0.063$, $P = 0.804$, $\eta_p^2 = 0.004$], and there was no interaction [$F(1,15) = 0.049$, $P = 0.828$, $\eta_p^2 = 0.003$]. Also, visually triggered saccades were almost twice as precise and more accurate than anticipatory saccades, as indicated by the smaller variability and smaller undershoot of the responses (see Fig. 6*A*). Because of the variability in participant SRT, four participants did not generate enough visually triggered saccades (*participants 9*, *13*, *19*, and *21*), and six other participants (*participants 2*, *5*, *7*, *10*, and *12*) did not generate enough anticipatory saccades between 8.3° and 9.3° (Fig. 6*A*) to analyze the peak velocity. For the remaining 12 participants, we contrasted peak velocity for saccades between 8.3° and 9.3° (see Fig. 6*B*.) We conducted a repeated-measures ANOVA with saccade category (anticipatory and visually triggered) and luminance (bright and dim) as factors. There was a main effect of saccade category [$F(1,11) = 15.8$, $P = 0.002$, $\eta_p^2 = 0.590$], meaning that the peak velocity for anticipatory saccades was lower than that for visually triggered saccades. There was no main effect of luminance [$F(1,11) = 0.3$, $P = 0.577$, $\eta_p^2 = 0.029$], but the significant interaction was significant [$F(1,11) = 9.193$, $P = 0.011$, $\eta_p^2 = 0.455$]. The interaction effect shows, as expected, that when saccades are anticipatory, the peak velocity is low regardless of the luminance of the target, but when saccades are visually triggered, saccades to a bright target have a higher peak velocity than saccades to a dim target.

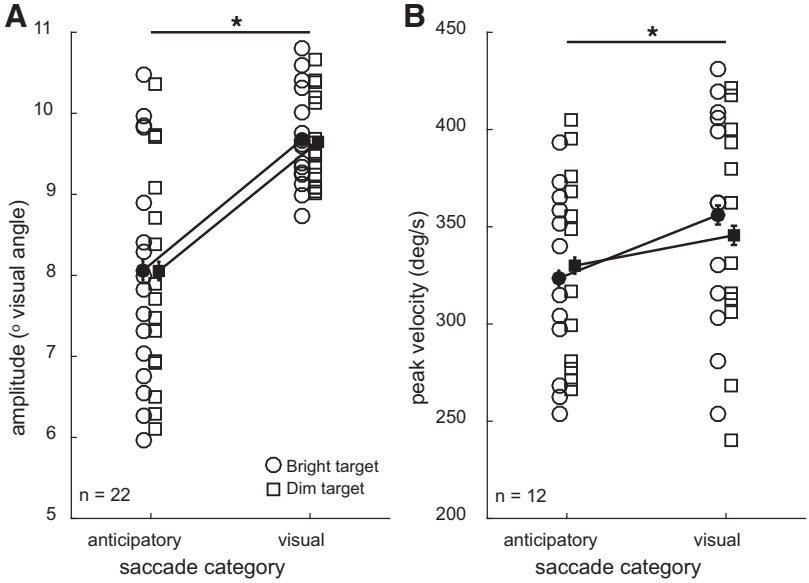

Fig. 6. *A*: amplitude distribution for all participants for the bright (○) and dim (□) targets (n = 22 participants, 14 female). *Main effect of saccade category: $F(1,15) = 41.073$, $P < 0.001$, $\eta_p^2 = 0.732$. *B*: interaction between the peak velocity of anticipatory and visually triggered saccades to bright (○) and dim (□) targets for all participants with similar numbers of saccades in all four categories (n = 12 participants, 7 female). Analysis was limited to saccades that were between 8.3° and 9.3° in amplitude. *Main effect of saccade category: $F(1,11) = 15.8$, $P = 0.002$, $\eta_p^2 = 0.590$.

DISCUSSION

In this article we provide a method that can be adopted to determine the SRT at which the transition from anticipatory saccades to visually triggered saccades takes place. We adopted luminance as the feature for a proof of concept to develop a translational method to show that minimal visual SRTs can be measured in humans. To maximize statistical power, we chose to present many trials at the two extreme luminance levels from the Marino et. al. (2015) study, for which the visual response onset latency and the earliest correct behavior SRTs correlated. This method makes it possible to determine, for each individual participant and each experimental condition, the lower bound cutoff for latencies of visually triggered saccades (the minimal visual SRT). We demonstrated the feasibility of this method by using two target luminance levels and applying two different approaches to calculate the minimal visual SRT. Furthermore, we showed that the minimal visual SRT was not fixed, but instead varied between participants and experimental conditions. We showed longer minimal visual SRTs during saccades to a dim target compared with a bright target. The implemented anticipation paradigm (including a gap and an auditory GO signal) deliberately elicited a large number of anticipatory saccades, which were, within the context of this study, considered all responses occurring before the visual target had been processed. This paradigm allowed us, using both correct and incorrect anticipatory and visually triggered responses, to determine the minimal visual SRT. We have confirmed that the minimal visual SRT should not be considered to be a constant and fixed value. It is suggested that when eye movement and vision-related research is being conducted, it is important to determine the minimal visual SRTs for each of the conditions tested. It is preferred to use a photodiode to record the precise timing of the stimulus onset.

The experimental design was successful in triggering a large proportion of anticipatory saccades. Keeping fixation duration fixed allowed participants to anticipate the time of target appearance. This is exactly what we were trying to achieve by having a fixed fixation duration, as well as a fixed 100-ms warning tone and a fixed 200-ms gap period before target appearance. All of these design features were specifically introduced to increase the proportion of anticipatory saccades. Our goal was to determine the minimum latencies for visually triggered saccades and not necessarily to investigate variability in human predictive responses. Varying the fixation time will slow participants down and reduce the number of anticipatory saccades (Badler and Heinen 2006; Heeman et al. 2017). This would make the estimate of the minimal visual response latency less accurate, because it would be harder to identify the kink, or transition of when triggering anticipatory saccades stops. It is indeed the predictability of the fixation offset that contributes to the high predictability and extremely short SRTs of the participants that we are specifically trying to exploit. The task for the participant is not one that can be performed automatically, and participants have to be made aware of this before and during the experiment. When participants respond only to the bottom-up cues of fixation offset and the auditory signal their responses, in general, will be too fast. This is indeed what a few of our participants showed (Fig. 3*B*, first 4 columns).

Based on what is known from studies involving single-cell recordings in monkeys, we expected a steep drop in the number of incorrect saccades to correlate with the SRT in which the transition from anticipatory to visually triggered saccades occurred. When the activation in the SC surpasses the saccadic response threshold, a saccade can no longer be prevented (Paré and Hanes 2003). As illustrated in Fig. 2, the rate of correct and incorrect responses for both the bright and dim conditions almost perfectly followed the same chance-level performance up to the point the minimal visual SRT was reached. At that point, the transition from chance-level performance to almost exclusively target-directed saccades occurred within a very small time window. This short transitional interval from chance level responses to mainly correct responses is indicative of the fast rise in activation of the visual-motor neurons, which correlates with the behavioral SRTs in Marino et al. (2015) and signifies the triggering of a saccade to the target. There was no evidence for a difference in the transitional interval (as indicated by the slope of the graphs in Fig. 2) between bright and dim targets. The lack of a difference is explained by the fact that a saccadic response is the outcome of a neural activation

that has surpassed the saccadic response threshold. Therefore, once the saccadic response threshold is surpassed, the change in correct and incorrect responses follows the same pattern regardless of luminance.

The current study strongly builds on the results reported in the neurophysiology study with three monkeys by Marino et. al. (2015). The Marino study comprehensively showed, using seven luminance levels, how luminance modulates both neural visual responses and behavioral saccadic response times and that these measures are strongly correlated, at least for the five brightest luminance levels that were employed. The longer minimal visual SRT in humans, as calculated using the Wilcoxon signed-rank test and by assessing the kink in the cumulative distribution, for dim targets compared with bright targets is remarkably consistent with neurophysiological recordings in monkey SC. The systematic shift in minimal visual SRTs between monkeys and humans, as shown in the results of the cross-species comparison (Fig. 5), is consistent with the idea that similar neural mechanisms are responsible for the increase in the onset time of the visual response as a function of decreasing luminance. It has been shown that the abrupt appearance of an object in the visual field results in transient activation in the SC retinotopic map. To make a saccade, the subsequent phasic activation that occurs when the element is salient needs to be driven past the saccadic response threshold (Paré and Hanes 2003). Bright targets elicited larger initial visual responses than dim targets, resulting in a faster rise to threshold and a lower minimal visual SRT for bright targets compared with dim targets. The difference in absolute values between the monkeys and humans has been observed previously (Fischer and Boch 1983; Fischer et al. 1984) and can be explained by the shorter distance of neural pathways with likely fewer connections between the photoreceptors and the extraocular motoneurons and by the fact that monkeys were highly over trained when performing the same experiment.

These findings also have implications for the detection of express saccades. Express saccades reflect the earliest visually triggered eye movements, because their SRT approaches the minimum afferent and efferent conduction delays that are required to transform a sensory retinal input into an oculomotor response (Fischer and Boch 1983; Fischer and Weber 1993; Paré and Munoz 1996). These saccades are considered to result from a previsual build-up of activity in the SC before a target appearance that merges with the visual transient produced by the appearance of a visual stimulus (Dorris and Munoz 1998; Dorris et al. 1997; Marino et al. 2015). The current data indicate that express saccades are not exclusively saccades that occur between roughly 70 and 130 ms after target onset, but that express saccades (defined as the fastest visual responses) can also occur at longer latencies when the visual target has specific properties, such as a relatively low luminance contrast. The difference between "early" and "late" express saccades is the time required to drive the summed activity past the saccadic response threshold (Bell et al. 2006; Marino et al. 2015).

Two behavioral definitions of express saccades have been adopted in the existing literature. First, it has been reported that express saccades form an independent peak in the SRT distribution that is separate from regular latency saccades (Fischer and Boch 1983; Fischer et al. 1984; Heeman et al. 2017). Even though bimodality seems to be more pronounced in monkeys than in humans, many studies, including the current one, do not report bimodality within the experiment (Edelman et al. 2007; Kingstone and Klein 1993; Reuter-Lorenz et al. 1991; Trottier and Pratt 2005; Wenban-Smith and Findlay 1991) or report differences between participants within the same experiment (Fischer et al. 1993). Also, a recent study has shown that bimodality can be influenced by changes in the design of the paradigm such as fixation jitter and auditory cues. When the minimal visual SRT is shifted, for example, due to a remote distractor, the bimodality is no longer observed (Heeman et al. 2017). Bimodality is therefore a poor indicator of the presence of express saccades in humans. Second, express saccades have been defined merely on the basis of their latency. However, as shown in the present study, use of a fixed lower bound cutoff for the analysis of visually triggered saccades of 70–90 ms after target appearance, as adopted in many previous studies (e.g., Bompas and Sumner 2009; Choi et al. 2016; Dhawan et al. 2013; Hollingworth et al. 2013; McSorley et al. 2017; Rothkirch et al. 2013; Silvis and Donk 2014; Tudge et al. 2018; van Zoest et al. 2017; White et al. 2013) is too rigid because we have demonstrated that the lower bound varies as a function of target luminance and is probably influenced by other external factors, as well, which is especially true for studies in which the stimulus saliency is manipulated. We have introduced a more reliable way to determine the lower bound cutoff for visually triggered saccades, signifying the lower bound limit of express saccade occurrence.

Anticipatory saccades had shorter amplitude than visually triggered saccades (Fig. 6*A*), which is in line with existing literature reporting that saccade amplitude of anticipatory saccades may be 75% to 90% shorter in amplitude than visually triggered saccades (Findlay 1981). Also, it has long been known that the peak velocity for saccades to visual targets is greater than the peak velocity for memory-guided saccades (no visual target) (Becker and Fuchs 1969; Bronstein and Kennard 1987; Hikosaka and Wurtz 1985; Smit et al. 1987). We therefore hypothesized that visual saccades should have a higher peak velocity than the anticipatory saccades in our participants. The results indeed confirm this hypothesis.

Whereas the differences between a short minimal visual SRT to a bright target and a longer minimal visual SRT to a dim target were consistent within all participants (Fig. 4*A*), this was not the case for the between-participant values of minimal visual SRT (Fig. 4*B*). We observed that the average SRT at which the transition from anticipatory to visually triggered saccades takes place varied up to 60 ms between participants. Researchers typically employ a cutoff of 70–90 ms to classify saccades as being anticipatory, but the current findings indicate that the minimal visual SRT strongly depends on the stimulus luminance that is used and mean that this cutoff is not always accurate. Now that the method has been established, of course, interesting aspects of minimal visual SRT can be explored in future investigations. The presented method can be used to study the minimal visual processing time of different stimulus features, intrastimulus timing, including auditory facilitation, under different experimental conditions, and within different participant groups in a noninvasive manner. It would be interesting to see how age or pathology modulate the saccade latency. In the current study, we showed both the large difference in minimal visual SRT between dim and bright targets and the short transitional interval from performance at chance level to mainly correct saccadic responses. We believe we have

fulfilled the aim of the study: to develop a behavioral paradigm that discriminates anticipatory and visually triggered saccades.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

J.H., S.V.d.S., and D.P.M. conceived and designed research; J.H. performed experiments; J.H. analyzed data; J.H. and D.P.M. interpreted results of experiments; J.H. prepared figures; J.H. drafted manuscript; J.H., S.V.d.S., D.P.M., and J.T. edited and revised manuscript; J.H., S.V.d.S., D.P.M., and J.T. approved final version of manuscript.

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