

The effects of bottom-up target luminance and top-down spatial target predictability on saccadic reaction times

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Abstract Saccadic reaction times (SRT) are composed of the sum of multiple processes, including bottom-up sensory processing, top-down goal oriented processing, and afferent and efferent conduction delays. In order to determine the timing dependencies and potential interactions between bottom-up and top-down processes on SRTs, we trained monkeys to perform several variants of visually guided saccade tasks. Bottom-up components of SRT were manipulated by varying target luminance from near detection threshold to supra-threshold ranges (i.e., 0.001–42.5 cd/m²). There was a significant reduction of mean SRT with increases in target luminance up to 3.5–17.5 cd/m². Luminance increases above these ranges produced significant increases in SRT when the target was within 6° from the fovea. Top-down components were assessed by manipulat-

ing spatial target predictability across blocks of trials using either 1, 2, 4 or 8 possible target locations. Decreasing spatial target predictability increased SRT across target luminances from 1 to 4 targets in the gap task, but then paradoxically decreased SRT again when there were 8 possible targets in both the gap and step tasks. Finally, a gap task (200 ms gap) was used to determine the dependence of target luminance on the magnitude of the gap effect. Decreasing target luminance significantly reduced the magnitude of the gap effect indicating that the gap effect is strongly influenced by bottom-up factors.

Keywords Stimulus intensity · Probability · Gap effect · Fixation offset effect · Pieron's law · Hick's law

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Introduction

The study of reaction times provides an important link between neural processing times and behavioral responses. Such “mental chronometry” enables the time course of sensory, motor, and higher level cognitive processing to be measured quantitatively (Posner 2005). Saccadic reaction times (SRT) are defined as the time required to initiate a saccade to a target after its appearance in the visual field. The sensory-to-motor transformations required to make a saccade to a sensory stimulus are modulated by bottom-up and top-down processes. Bottom-up processes depend on the physical properties of the visual target stimulus, which includes the onset and offset stimuli, and influences the time to stimulus detection. Top-down processes involve prediction, and enable the prior expectation and preparation of the saccadic response to influence saccadic planning. The purpose of this study is to better understand the various contributions of these processes to variability in SRT.

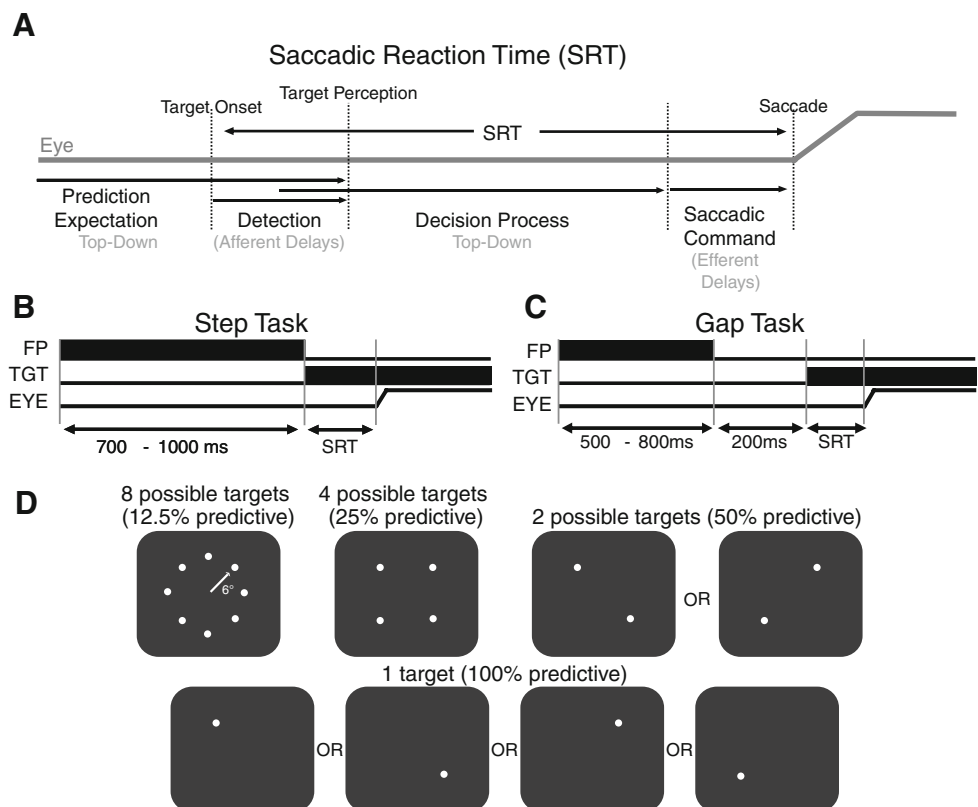
SRT distributions can be characterized by multiple modes, a fast mode of express saccades (traditionally reported ~ 80 ms in monkey) and a slower mode of regular saccades (Fischer and Boch 1983). Express saccade latencies approach the minimum afferent and efferent processing delays inherent to the visual and oculomotor system, whereas regular latency saccades exceed these minimums (Carpenter 1981; Dorris et al. 1997; Dorris et al. 2007). Although a small fraction of the increased latency for regular saccades is caused by inherent sensory noise, the bulk of regular SRTs are determined by several underlying subprocesses (Thompson et al. 1996; Carpenter 2004) including: prediction/expectation processes, afferent detection processes (retinal processing and afferent conduction), decision processes, and the efferent transmission of the saccadic motor command to the brainstem burst generator (Fig. 1a).

Here, we manipulate top-down prediction/expectation processing time by varying spatial target predictability systematically; and we manipulate bottom-up detection processing time by varying target luminance. We then quantify how these different top-down and bottom-up factors affect SRT processing. The resulting implications are important for understanding the minimum processing delay cutoffs required for visually triggered saccades, and the magnitude of behavioral benefits and deficits resulting from specific top-down and bottom-up factors.

The relationships between stimulus intensity, contrast, and reaction times have been investigated previously across different sensory modalities (vision, audition, cutaneous touch, taste and smell) in both humans (Doma and Hallett 1988; Jaskowski and Sobieralska 2004; Ludwig et al. 2004; White et al. 2006) and monkeys (Bell et al. 2006; Boch et al. 1984). Many of these studies have shown a consistent relationship between stimulus intensity and reaction time that is independent of the sensory modality under study. Pieron's law (Pieron 1952) mathematically describes these observed relationships as a hyperbolic decay function whereby as stimulus intensity increases, the behavioral reaction time decreases until some asymptotic threshold is attained. Through the systematic manipulation of target luminance from near threshold to supra-threshold ranges, we hypothesize an asymptotic decrease of SRT latency with increasing target luminance in agreement with Pieron's law.

The latency of decision processes can be reduced by top-down predictive processes that alter the state of neural networks prior to target appearance (Basso and Wurtz 1998; Dorris and Munoz 1998). Task predictability can be influenced by both temporal and spatial predictability (independent of the response modality under study). Hick's law (Hick 1952) mathematically describes these observed relationships between response latency and spatial stimulus

Fig. 1 **a** Schematic of the component processes underlying saccadic reaction time (SRT) including processing stages and efferent and afferent conduction delays. SRT is defined as the time required to initiate a saccade to a target after its appearance. **b, c** Schematic representation of temporal events in the step and gap tasks for the fixation point (FP), target (TGT) and eye position. **d** Schematic of the spatial target locations used within daily blocks of trials



response uncertainty as a log function of the number of response alternatives. However, some exceptions to this law have been reported in human studies, including oral and pointing responses to light (Brainard et al. 1962; Morin and Forrin 1962; Fitts 1964), as well as visually guided pro-saccades (Kveraga et al. 2002). Task predictability (both spatial and temporal) reduces mean SRT by incorporating prior knowledge to prepare saccadic commands prior to the appearance of a target, or biasing specific visual sensory signals (Basso and Wurtz 1997, 1998, Dickov and Morrison 2006; Dorris and Munoz 1998). Once altered, the sensory responses to predicted targets in visuomotor structures are optimized relative to unpredicted or unexpected targets. Through manipulation of target predictability, we hypothesize that increasing spatial target predictability will reduce SRT.

The gap task combines both bottom-up and top-down factors. The top-down factors include spatial target predictability (the probability of where in space targets may appear in the visual field) (Dorris and Munoz 1998). The bottom-up factors include the disappearance of the fixation point which acts to remove visual input from the fovea, thereby reducing competition and lateral inhibition of peripherally appearing targets (Dorris and Munoz 1995; Trappenberg et al. 2001). The effect of the gap has been shown previously to produce a reduction in SRT and increase the proportion and probability of express saccades (Boch et al. 1984; Fischer 1986; Fischer and Boch 1983; Pare and Munoz 1996). It has been shown previously that spatial target predictability significantly affects the magnitude of the gap effect (Basso and Wurtz 1997); however, bottom-up target luminance has not been shown to impact the gap effect (Reuter-Lorenz et al. 1991).

The specific goals of this study are: (1) to quantify the influences of bottom-up and top-down factors on saccadic latency in order to better understand their individual contributions to reaction time, (2) to characterize the minimum latency cutoffs for visually triggered saccades by varying bottom-up luminance in order to systematically characterize afferent sensory processing delays, and (3) to utilize bottom-up target luminance and top-down target predictability as a tool to quantify the underlying factors composing the gap effect. These data have been presented previously in abstract form only (Marino and Munoz 2005).

Methods

All experimental procedures employed were approved by the Queen's University Animal Care Committee and met the requirements set out by the Canadian Council on Animal Care. Experiments were conducted in 2 male monkeys (*Macaca mulatta*, weight: 8, 16 kg; age: 6, 9 years,

respectively). Eye position was recorded using the magnetic search coil technique (Robinson 1963). Surgical methods for preparing animals for head fixed eye movement recordings have been described previously (Marino et al. 2008). Briefly, monkeys underwent a single surgical session under aseptic conditions. Animals were sedated for surgery by an injection of ketamine-hydrochloride (6–10 mg/kg IV) followed with an injection of glycopyrrolate (0.013 mg/kg) to reduce salivary secretions. Anesthesia was initiated with a bolus of propofol (2.5 mg/kg) and maintained during the surgery with 1.5–2.5% isoflurane gas while heart rate, respiratory rate, pulse oximetry and temperature were monitored. A stainless steel head post was attached to the skull via an acrylic implant anchored to the skull by stainless steel screws. Eye coils were implanted between the conjunctiva and the sclera of each eye (Judge et al. 1980). The leads from each coil were passed under the scalp to external connector plugs, which were embedded within the acrylic implant. Post surgery, monkeys received analgesics, antibiotics and anti-inflammatory (buprenorphine hydrochloride 0.01 mg/kg, enrofloxacin 5 mg/kg, ketoprofen 1–2 mg/kg (2 mg/kg day 1, 1 mg/kg day 2) for discomfort. Behavioral training began at least 4 weeks post surgery.

Visual stimuli and behavioral tasks

Monkeys were trained to perform a variety of controlled oculomotor saccade tasks for liquid water reward. Monkey W received approximately 3–4 months of training prior to data collection, and monkey O received over 5 years of training on various oculomotor tasks prior to data collection. Real-time control of the experimental task and visual display was achieved using REX version 6.0 (Hays et al. 1982). Monkeys were seated in a primate chair 53 cm away from a CRT monitor. The monitor spanned 32° of horizontal angle and 25° of vertical angle from the center of the screen. SRT and eye position were recorded from each monkey while they performed saccade tasks. With the exception of the controlled presentation of visual stimuli, all monkeys performed the tasks within a darkened environment. Dark adaptation was prevented by dimly illuminating the monitor screen during the inter-trial interval (ITI) which varied randomly between 800 and 1500 ms.

In the step saccade task (Fig. 1b), each trial began with the presentation of a blank screen. After 250 ms, a 0.25° circular grayscale fixation point (FP; 3.5 cd/m²) appeared against a dark background (0.0001 cd/m²) at the center of the display monitor. After fixation point appearance, the monkeys had 1,000 ms to move their eyes and fixate the fixation point before the trial would be aborted as an error. Fixation of the central FP was maintained for a variable period (700–1,000 ms) before a circular 0.25° grayscale

target appeared at 6° eccentricity from the FP. The target could appear in the horizontal, vertical or oblique direction depending on the total number of possible target locations presented in the experimental block (Fig. 1d). Once the target appeared, the monkey was given 1,000 ms to initiate a saccade to the target. If fixation was broken before the target appeared, or the monkey did not complete a saccade within a 2.5° (of visual arc) window around the presented target, the trial was scored as an error and analyzed separately. A square analog window centered on the fixation point and target ensured eye position remained within 2.5° of the fixation point and the target during all correct trials. Total trial duration of a correct trial ranged from approximately 1 to 2 s depending on the variability of fixation duration and SRT.

The gap saccade task condition (Fig. 1c) was identical to the step task except a 200 ms period of darkness (gap) was inserted into each trial between fixation point disappearance and target appearance (Saslow 1967). During the gap task, the monkey was required to fixate for a duration of 500–800 ms before the 200-ms gap, which ensured that the total variable period of fixation was identical to the 700–1,000 ms fixation period used in the step task.

Fixation point luminance was held constant at 3.5 cd/m^2 and seven distinct target luminances (0.001, 0.005, 0.044, 0.4, 3.5, 17.5, and 42.5 cd/m^2) were randomly interleaved within each block of trials. Luminance was measured with an optometer (UDT instruments, model S471) that was positioned directly against the screen of the monitor and centered on the stimulus.

Spatial target probability was manipulated within each block of trials by fixing the total number and possible locations of the targets. Blocks of 1, 2, 4, or 8 possible target locations were used in this study (Fig. 1d). Within a block, targets would appear at each of the possible target locations with equal probability such that the probability of target appearance was 100, 50, 25, or 12.5%, respectively. In blocks with 1, 2, or 4 potential target locations, targets were presented at oblique 45° angles with an eccentricity of 6° from the fixation point. Blocks with 1 or 2 potential targets were counterbalanced such that all of the target locations represented in the 4 potential target condition were recorded. When 2 potential targets were presented, the targets appeared in diagonally opposed locations. Blocks with 8 potential targets included 4 additional target locations located at 6° eccentricity along the horizontal and vertical axes.

In some experiments, we manipulated target eccentricity and luminance within the same block of trials. Targets were randomly presented at eccentricities of 2° , 6° , 10° and 20° from the central FP along oblique 45° angles. The same seven target luminances were randomly interleaved within each block.

Data collection began only after overall training performance on the required tasks exceeded an accuracy of 85% for all initiated trials. Tasks (gap vs. step) and spatial predictability manipulations were held constant during every block of trials presented within each daily recording session. The presentation of each experimental condition followed a repeating 8-day protocol schedule (4 days of the gap saccade task followed by 4 days of the step saccade task). Within each task (gap or step), target probability followed a repeating 4-day schedule (100, 50, 25, 12.5%). An average of 664 ± 64 , 509 (SE, standard deviation) and 412 ± 32 , 253 (SE, standard deviation) trials per condition were recorded from monkey O and W, respectively. A total of 41,184 and 25,942 correct trials were recorded from monkey O and W, respectively (see Table 1).

Data analysis

The beginning and end of fixation periods and saccadic eye movements were calculated automatically using custom Matlab (Matlab 6.1, Mathworks Inc) software during offline analysis. The start and end of saccades were determined from velocity and acceleration template matching criteria; verified offline by the experimenter, and corrected when necessary. In the eight possible target condition block, SRTs to horizontal and vertical targets were eliminated from further analysis to ensure only identical oblique saccade vectors were compared between target probability blocks. Anticipatory responses (see below) and long latency SRTs, greater than three standard deviations from the mean, were removed from further analysis.

To determine the shortest SRT for visually-driven saccades, we analyzed SRT histograms (15 ms bins) aligned on target appearance when two equally possible target locations were presented within blocks of gap saccade trials. This temporal accuracy of the anticipatory range was achieved (i.e., minimum resolution of 15 ms) due to the large sample size obtained. The distribution of SRTs for correct saccades made into the target window was compared to the SRT distribution for direction errors, i.e., saccades made incorrectly to the opposite target location. The value of each pair of correct and incorrect bins was then compared at every target luminance presented. Anticipatory saccades occurred with equal probability to either of the two target locations (50% predictable), whereas the earliest visually guided movements were biased toward the correct target location. The first bin in both distributions where the monkey made significantly more correct trials than direction errors determined the end of the anticipatory saccade period and denoted the minimum time required for visual information from target appearance to propagate through the visual system to bias saccade initiation (Dorris et al. 1997; Edelman and Keller 1996; Fischer and Boch 1983;

Table 1 Total correct SRT trials recorded per condition

	Target luminance (cd/m ²)						
	0.001	0.005	0.044	0.4	3.5	17.5	42.5
Monkey O							
1 Target step task	485	565	601	584	593	595	600
2 Target step task	316	374	371	372	383	393	390
4 Target step task	273	360	364	375	372	370	367
8 Target step task (oblique saccades only)	172	177	194	200	190	192	201
1 Target gap task	376	607	685	722	752	739	759
2 Target gap task	713	1,644	1,858	1,911	1,936	1,958	1,951
4 Target gap task	343	588	600	615	630	608	617
8 Target gap task (oblique saccades only)	232	290	311	311	334	325	317
4 Eccentricity gap task	541	1,098	1,219	1,257	1,286	1,313	1,309
Monkey W							
1 Target step task	210	269	271	283	281	286	262
2 Target step task	345	443	451	457	463	443	450
4 Target step task	391	420	445	448	443	444	400
8 Target step task (oblique saccades only)	148	155	154	142	159	143	138
1 Target gap task	136	280	288	288	298	288	266
2 Target gap task	393	973	1,006	1,031	1,022	987	982
4 Target gap task	232	553	558	572	582	541	569
8 Target gap task (oblique saccades only)	113	154	135	134	136	140	125
4 Eccentricity gap task	311	611	663	650	665	678	638

Pare and Munoz 1996). Bin sizes between correct and direction error saccades were compared using running binary sign tests. If fewer than 10 saccades were represented within the first consecutive and statistically greater SRT bin, additional bins were included until the total number of saccades represented in the bins exceeded 10 counts in order to compensate for the smaller sample sizes present at some target intensities.

The gap effect was calculated from the difference in mean SRT between the step and gap tasks across each spatial target predictability condition. Differences in mean SRT were used to assess the magnitude of the gap effect across each of the target luminance and spatial predictability conditions tested.

Error rates were calculated from the subset of incorrect trials in which the target was presented. Early aborted trials where the monkey failed to fixate the FP at the beginning of the trial were eliminated from further analysis as they were not representative of active task participation. Error trials were included in the error rate calculation when the monkey initiated a trial by actively fixating the fixation point at the start of a trial and then holding fixation until the target was presented. Trial types included in the error rate calculations were: (1) anticipation errors (saccades made after the target appearance, but before luminance-specific afferent

detection delays allowed it to be perceived; see “Results”); (2) saccadic errors (incorrect saccades initiated after target was perceived that landed outside the target window); (3) correct saccades initiated with SRTs more than 3 standard deviations above the mean; (4) trials where no saccade was made. The overall breakdown of the error rate was 35% anticipation errors, 52% saccade errors, 10.5% removed trials where the SRT was above 3 standard deviations above the mean, and 2.5% trials where no saccade was made. Uninitiated trials that were not attended to by the monkey and fixation errors made prior to target appearance were eliminated from further analysis. Percent error rate was compared and analyzed using a *z* test for proportions.

Saccade endpoint accuracy was calculated as the absolute position error between the saccadic endpoint (mean eye position during the first 10 ms of fixation immediately following the saccade) and spatial target location at each of the target luminances tested. If a small corrective saccade occurred (less than 1% of trials), the endpoint of the initial saccade landing within the 2.5° window was used. Saccadic endpoint accuracy error was calculated as the mean of each of the absolute endpoint accuracy errors to the four oblique target locations. Saccade endpoint variability was calculated as the variance of the absolute endpoint accuracy error. Mean saccade endpoint variability was calculated from the

distribution of variances. Analyses on endpoint variance were performed on the mean variance across sessions using a *t* test. Repeated measures ANOVA (trials collapsed across experimental session) were applied to the data to determine statistical significance and trend analyses. For factors with more than two levels, we performed post hoc Bonferroni corrected pairwise *t* tests with alpha set at 0.05.

Results

Bottom-up effects of target luminance on SRT

Figure 2 illustrates the SRT distributions of correct saccades obtained from both monkeys for each of the seven randomly presented target luminances. These data represent all gap trials where the target always appeared in the same spatial location within a block of trials. As the target luminance increased, SRT decreased until a minimum or fastest SRT was reached. Further increases in target luminance produced longer mean SRTs, and resulted in a U-shaped functional relationship between target luminance and SRT that violated Pieron's law (Pieron 1952). Several of the SRT distributions, especially from monkey W, showed evidence of multiple modes. According to the classification schemes developed by Fischer and colleagues (Fischer and Boch 1983; Fischer and Weber 1993; Weber et al. 1993), the earliest mode occurring around 80–100 ms corresponded to express saccades and later modes corresponded to regular and late regular saccades. Although the proportions of express saccades (see Fig. 2 initial mode of SRT histograms) were small within the SRT distributions of both monkeys, they scaled with target luminance such that the proportion of express saccades increased with increasing target luminance.

Both monkeys showed the same main effect of target luminance (repeated measures ANOVA monkey O: $F(6,498) = 1,256.5$; $P < 0.01$, monkey W: $F(6,330) = 305.9$, $P < 0.01$). Bonferroni corrections were applied to the data and trend analysis determined that quadratic functional trends were present across luminance conditions from the data of both monkeys in the gap and step task conditions (Fig. 3a). This indicates the statistical existence of a U-shaped functional relationship between target luminance and mean SRT. Furthermore, pairwise comparisons from both monkeys and task conditions also showed that the mean SRT for the brightest target luminance of 42.5 cd/m^2 was significantly slower than the second brightest target luminance 17.5 cd/m^2 (Bonferroni corrected $P < 0.05$) in all but the step task for monkey O where the trend was present but did not achieve significance. The target luminance that produced the fastest mean SRT differed between the two monkeys tested. Monkey O had the fastest SRT at a target luminance of

17.5 cd/m^2 , while monkey W had the fastest SRT at a dimmer target luminance of 3.5 cd/m^2 . Despite this minor inter-subject difference, both monkeys produced a significant U-shaped functional relationship with target luminance across all spatial target probabilities. SRTs of monkey O were consistently faster than those of monkey W across all luminance and target predictability conditions (mean difference 31 ms, repeated measures ANOVA, $F(1,152) = 93.4$, $P < 0.01$), which may have resulted from the individual differences in overtraining between each monkey.

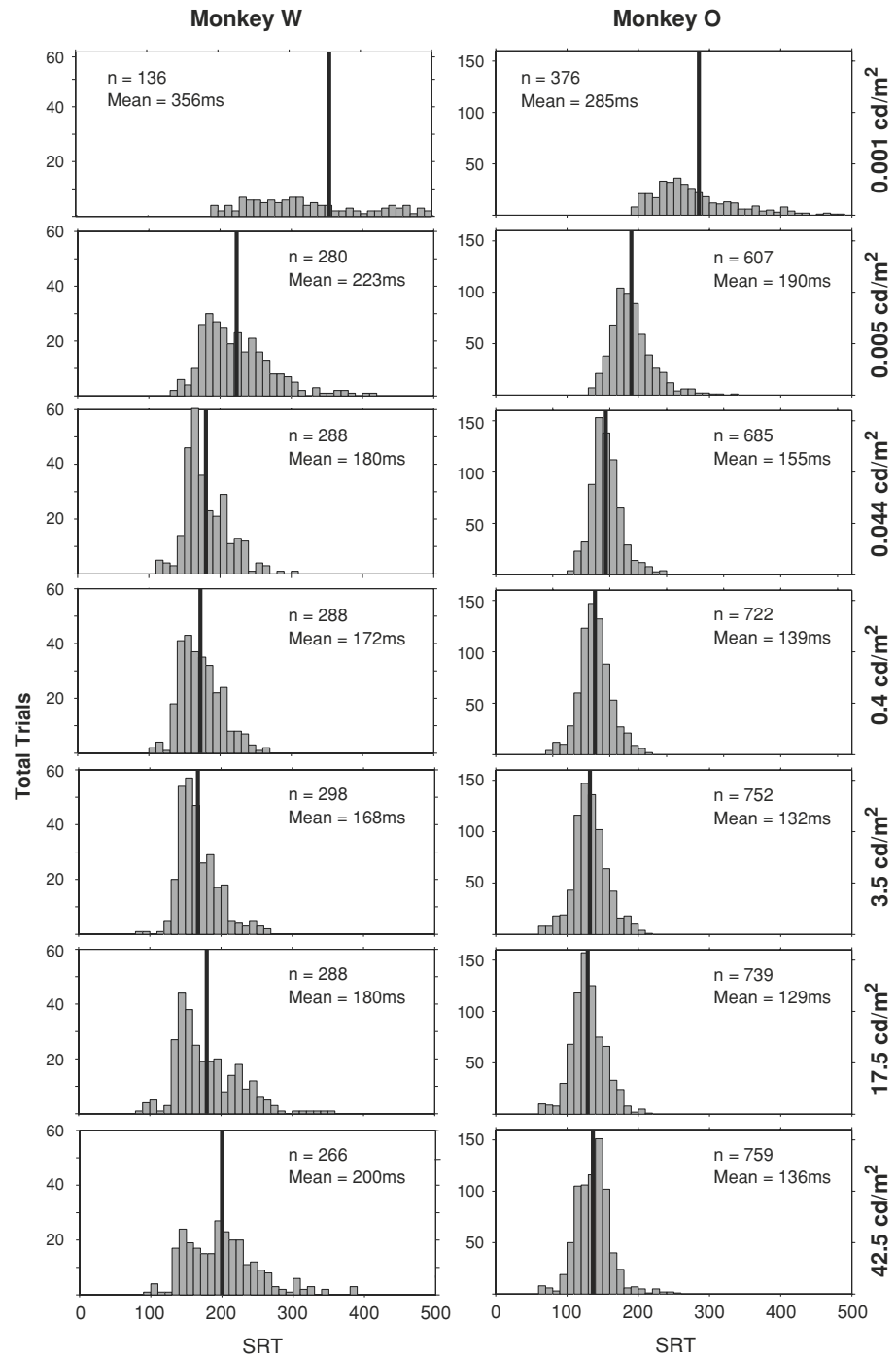
Bottom-up effects of target eccentricity and luminance on SRT

In order to further explore the paradoxical slowdown of SRT at the brightest luminances, we investigated whether this effect was related to the spatial position of the target relative to the fovea. We hypothesized that this effect could be related to spatial interactions (e.g., Trappenberg et al. 2001) or competition between foveal and parafoveal regions that were stimulated by the bottom-up target signal and the actively fixated FP. We analyzed the difference in SRT between the brightest and second brightest targets to assess whether the magnitude of the slowdown was related to target eccentricity. Figure 4 plots this difference in SRT between the two brightest luminances for targets presented at four different target eccentricities (2° , 6° , 10° , 20°) in the gap task. As target eccentricity increased, the magnitude of the paradoxical increase in SRT at the brightest luminance was minimized. This correlation was significant ($r = -0.83$, $P = 0.01$) when collapsed across both monkeys. These data indicated the paradoxical slowdown of SRT with increasing luminance at the brightest targets was related to target eccentricity.

Anticipatory saccade cutoff times

Consistent with previous research (Bell et al. 2006), the range of anticipatory saccades varied systematically with target luminance. Figure 5 illustrates the anticipatory cutoff ranges calculated for both monkeys at each target luminance. The bottom horizontal error bars represent the start of the first bin where correct saccades outnumber direction errors by simple bin size comparison and remained larger for the duration of the distribution. The solid triangle denotes the start of the first consecutive bin where the number of correct saccades significantly outnumbered direction errors by a running binary sign test ($P < 0.05$). At the dimmest target luminance, the anticipatory cutoff time was much longer and included values that extended well beyond the ranges previously described in monkey for regular and express saccades (Bell et al. 2006; Boch and Fischer 1986; Boch et al. 1984; Pare and Munoz 1996).

Fig. 2 SRT histograms (15 ms bins) from both monkeys recorded in the gap task when only one possible spatial target location was presented during an experimental session. The vertical black line represents the mean SRT from the distribution

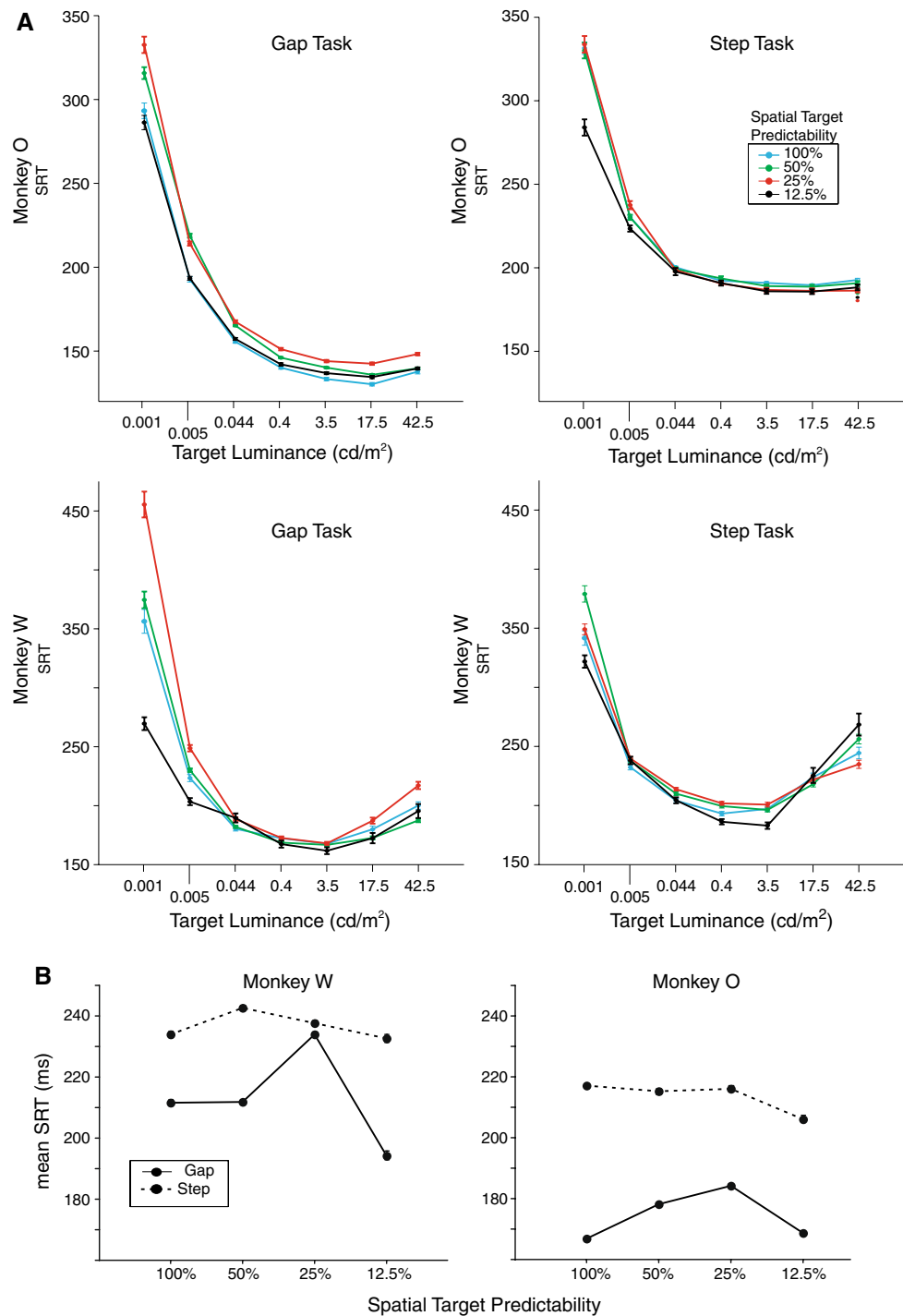


Top-down effects of spatial target predictability

Figure 3a shows the mean SRTs for each monkey for all spatial target predictabilities and target luminance conditions during the gap and step tasks. The characteristic U-shaped function in SRT was maintained across all spatial target probability conditions in violation of Piéron’s Law except in the step task for monkey O. Both monkeys showed the same main effect of spatial target predictability collapsed across the gap and step tasks (repeated measures ANOVA; monkey

W: $F(3,55) = 3.99, P < 0.012$; monkey O: $F(3,83) = 3.6, P < 0.016$). Figure 3b plots mean SRT across spatial target predictability collapsed across target luminance in the gap and step tasks. Both monkeys O and W demonstrated an inverted U-shaped trend (determined by a repeated measures ANOVA trend analysis) of mean SRT that increased at spatial target probabilities ranging from 1 to 4 possible targets (all conditions except the step task for monkey O) and then decreased again when 8 possible target locations were employed (all monkeys and conditions). The decrease in

Fig. 3 Effects of spatial target probability and target luminance on mean SRT (\pm SE) for the gap (left column) and step (right column) task for monkey O (top row) and monkey W (middle row). **a** Colored lines denote spatial target predictabilities of 100% (blue 1 possible target location), 50% (green 2 possible target locations), 25% (red 4 possible target locations), and 12.5% (black 8 possible target locations). **b** Effects of spatial target predictability on mean SRT collapsed across target luminance for monkey W (left column) and monkey O (right column). Solid lines denote data from the gap task and broken lines denote the step task



mean SRT between 4 and 8 possible targets was not anticipated a priori and appeared to violate Hick's Law. This was statistically significant in post hoc Bonferroni corrected pairwise comparisons in both monkeys across the gap (monkey W: mean difference 39.7 ms, $P < 0.01$, monkey O, mean difference 15.5 ms, $P < 0.01$) and step tasks (monkey W: mean difference 4.9 ms, $P = 0.021$, monkey O, mean difference 9.4 ms, $P < 0.01$).

Gap effect

In order to examine the robustness of the top-down and bottom-up effects, saccades following different levels of fixation disengagement were generated using gap and step tasks.

The effect of the gap is to produce a reduction in SRT and increase in the proportion and probability of express saccades (Boch et al. 1984; Fischer 1986; Fischer and Boch

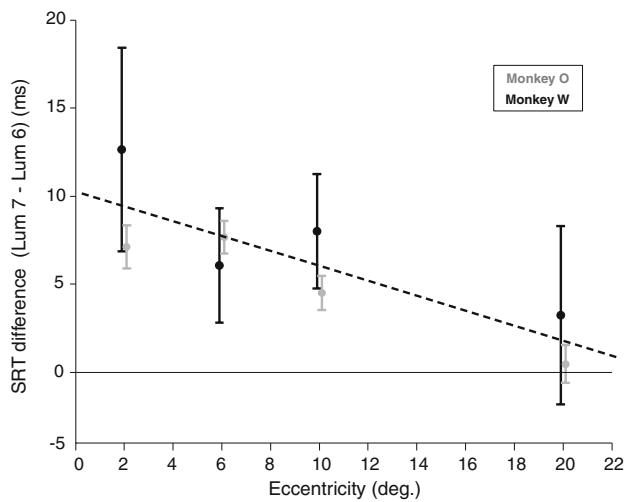


Fig. 4 Difference in SRT between the brightest (42.5 cd/m^2) and second brightest (17.5 cd/m^2) targets across four different target eccentricities (2° , 6° , 10° , 20°) in the gap task. SRT data was collapsed across the four oblique saccade vectors used in the previous luminance experiment. Data for monkey O (grey) and monkey W (black) are shown. The dashed line denotes the linear regression through all data points from both monkeys ($r = -0.83$, $P = 0.01$). Error bars denote standard error of the mean. Data are slightly staggered on the x -axis for readability

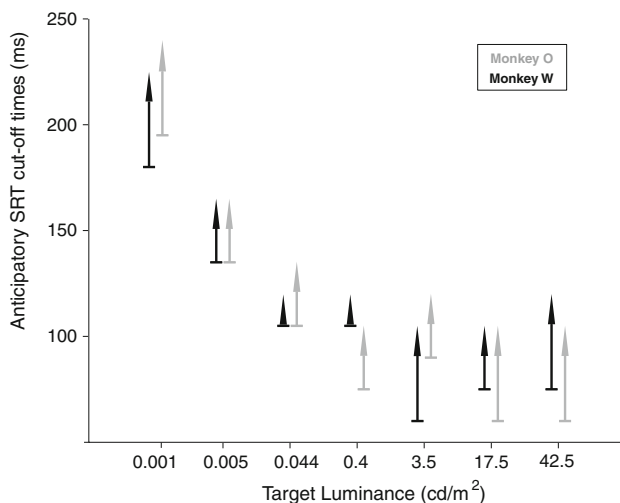


Fig. 5 Anticipatory SRT cutoff times for monkey O (grey) and monkey W (black) calculated in the gap task when two potential spatial target locations were presented. The lower horizontal line indicates the beginning of the first bin where the number of correct SRTs consistently outnumbered the number of error SRTs within the corresponding bin. The solid triangle indicates the beginning (bottom) and end (tip) of the first bin where the correct SRTs significantly outnumber error SRTs by a running binary sign test ($P < 0.05$)

1983; Pare and Munoz 1996). A significant gap effect (step SRT–gap SRT) was found in each monkey (repeated measures ANOVA; monkey W: $F(1,55) = 25.1$, $P < 0.01$; monkey O: $F(1,83) = 172.6$, $P < 0.01$) when spatial predictability and luminance conditions were collapsed. The gap

effect also interacted significantly with both target luminance and spatial target predictability (Fig. 6). Post hoc pairwise comparisons showed that a significant gap effect was found in 26 of 28 conditions (7 target luminances \times 4 target probabilities) for monkey O and 24 of 28 conditions for monkey W ($P < 0.05$, Bonferroni corrected) (Fig. 6a). The magnitude of the gap effect depended on target luminance (Fig. 6b). As target luminance increased, the magnitude of the gap effect increased. For monkey W, the gap effect reached a negative value at the dimmest target luminance indicating that the gap effect was eliminated as the target luminance approached detection threshold. The magnitude of the gap effect also varied across the different spatial target predictabilities (Fig. 6c); however, because these effects were not consistent across both subjects they were not analyzed further.

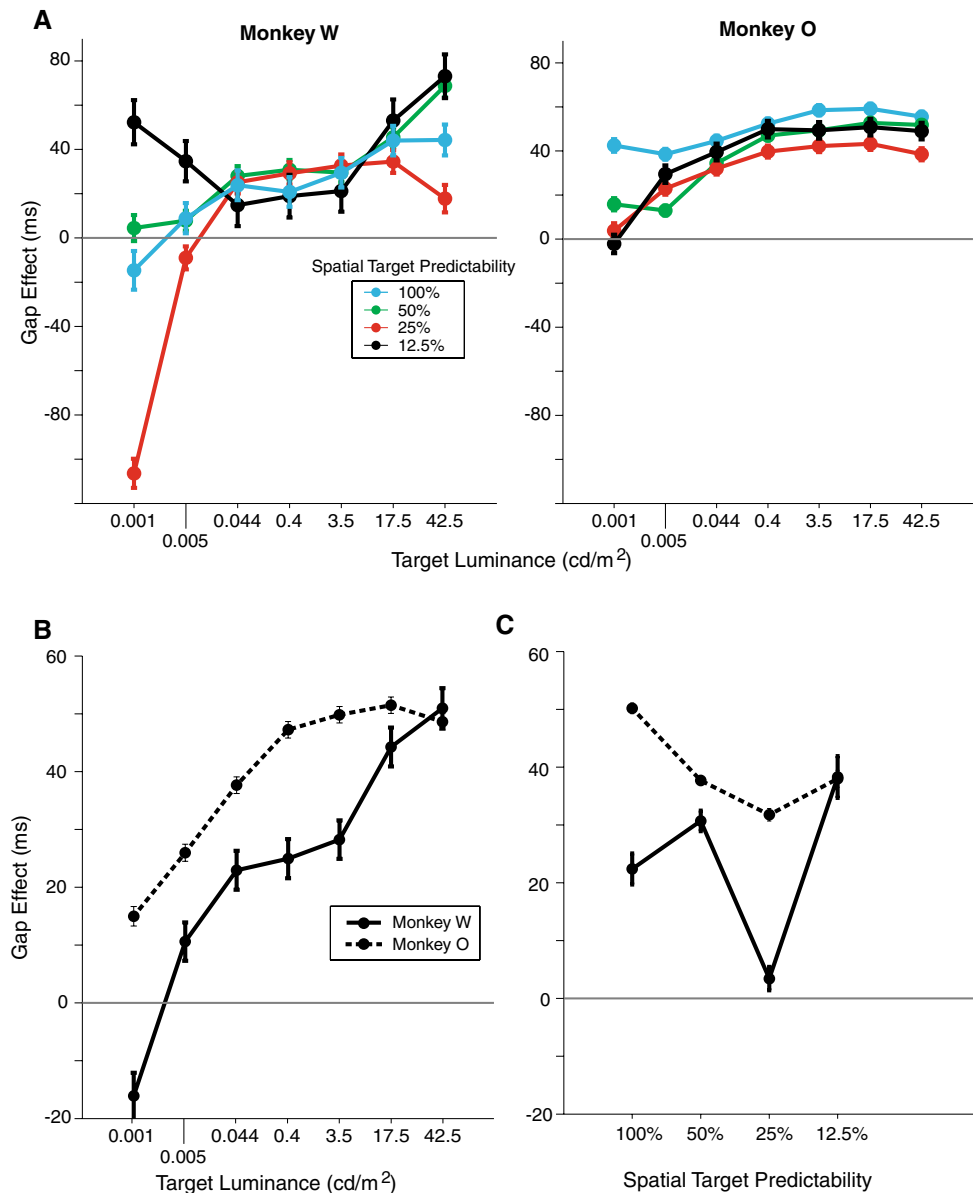
Speed–accuracy and speed–error rate trade-offs

Two possible behavioral performance trade-offs that could affect SRTs in our experiments are speed/saccadic endpoint accuracy trade-offs and speed/error rate trade-offs. We analyzed saccadic endpoint accuracy (Fig. 7a, b), saccadic endpoint variance, and error rate (Fig. 7c, d) to determine whether they could account for either the paradoxical increase in SRT at the brightest luminances or the paradoxical decrease in SRT that occurred when switching from 4 to 8 possible target locations. We hypothesized that if these paradoxical effects were driven by speed/accuracy or speed/error rate trade-offs, then any observed decrease in SRT would come at the behavioral cost of decreasing saccadic accuracy, increasing saccadic variance or increasing error rate. Likewise any observed increase in SRT would yield a behavioral benefit of increasing saccadic accuracy, decreasing saccadic endpoint variance or decreasing error rate.

Like mean SRT, saccadic endpoint accuracy error formed a U-shaped relationship with target luminance (Fig. 7a, b). Speed–accuracy trade-off relationships were not found with changes in target luminance as saccadic endpoint accuracy error covaried with mean SRT. Saccadic endpoint accuracy error also did not account for the paradoxical decrease in SRT from the 4 to 8 possible target conditions as endpoint accuracy error did not increase from 4 to 8 possible targets (Fig. 7a, inset).

The paradoxical increase in SRT at the highest target luminances was also not accounted for by endpoint variance, as it did not significantly decrease at the brightest intensity. There was a small increase in the variance of the saccadic endpoint between the 4 and 8 target spatial predictability conditions (monkey O: $0.015 \pm 0.009^\circ$; monkey W: $0.005 \pm 0.01^\circ$) that was significant for monkey O (t test, $P < 0.05$), but it is unclear whether the magnitude of

Fig. 6 a Gap effect for monkeys O and W (mean step–mean gap SRT broken down by monkey, task, spatial target predictability and target luminance). 100% (blue 1 possible target), 50% (green 2 possible targets), 25% (red 4 possible targets), and 12.5% (black 8 possible targets). **b, c** Same data collapsed across spatial target predictability (left panel) and target luminance, respectively (right panel). Error bars represent standard error of the mean



this increase in variability was sufficient to account for the decreases in mean SRT recorded.

Both monkeys performed proficiently across all tasks and conditions. The poorest performance, which occurred at the dimmest target luminance (<25% errors, Fig. 7c, d), was significantly above chance and indicated that all target luminances were above the detection threshold. A higher percentage of error trials were recorded during the gap task (6.3% increase) due to an increased proportion of anticipation saccades. Like saccadic endpoint accuracy and variance, error rates significantly increased at the dimmest target luminances (Fig. 7c, d; gap, 9.2% increase; step, 1.4% increase), but did not increase at the brightest luminances. Increases in error rate from 4 to 8 targets were seen (gap, 5.2% increase; step, 6.6% increase), and were significant within each monkey and task condition (monkey

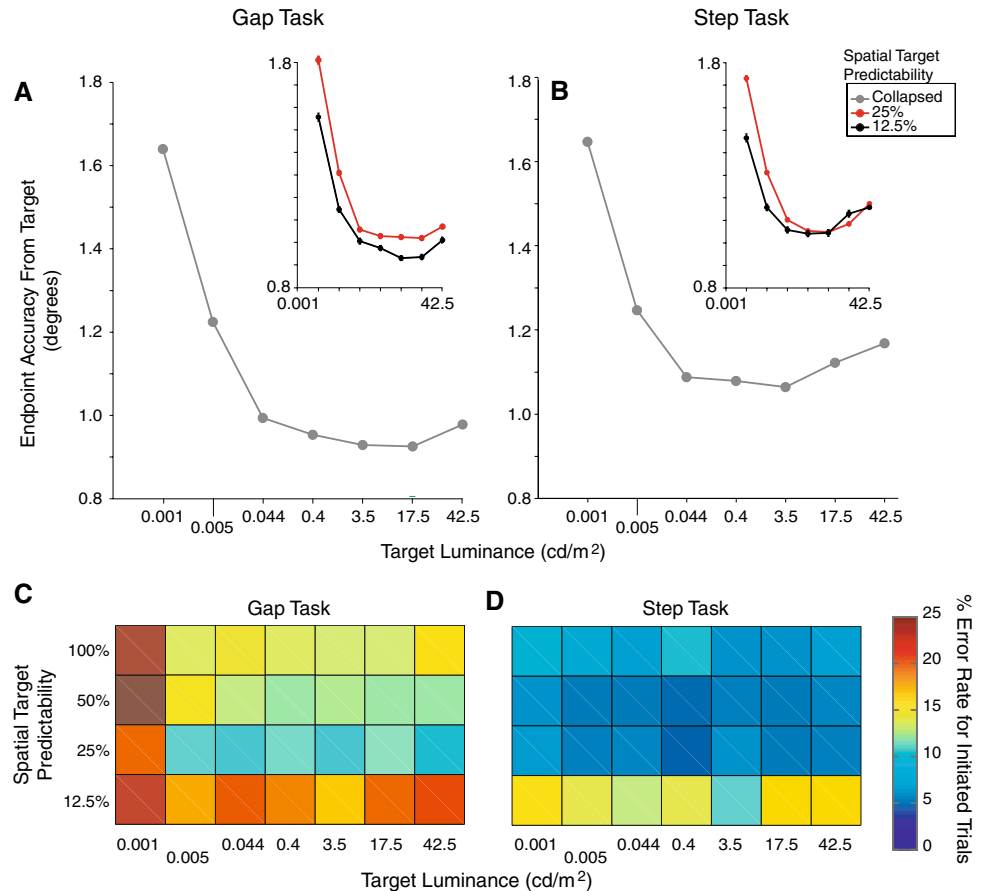
W: gap, $z = 4.57$, $P < 0.0001$; step, $z = 10.49$, $P < 0.0001$; monkey O: gap, $z = 13.05$, $P < 0.0001$; step, $z = 5.11$, $P < 0.0001$).

In summary, neither speed/accuracy nor speed/error rate trade-offs accounted for the observed paradoxical behavioral effects of increased SRT at the brightest luminance. Significant increases in percent error rate were seen from 4 to 8 possible targets that could indicate that the paradoxical behavioral effects of decreased SRT from 4 to 8 possible target locations could have resulted from a speed/error rate trade-off.

Discussion

SRT was significantly modulated by luminance and the spatial predictability of target location. The relationship

Fig. 7 Saccade endpoint accuracy error (**a, b**) collapsed across both monkeys in the gap and step tasks across all target luminance conditions. *Inner panel* endpoint accuracy collapsed across all spatial target predictabilities (*grey*). *Inner panel* endpoint accuracy for the 25% (*red* 4 possible targets), and 12.5% (*black* 8 possible targets) target predictability conditions. The 12.5% condition represents SRT data from oblique targets only. **c, d** Percent error rate for initiated trials from both monkeys in the gap and step tasks across all target luminance and spatial target predictability conditions



between target luminance and SRT was U-shaped and violated Pieron's law (Pieron 1952) when the target was within 6° of the fovea (Figs. 3a, 4). When the targets were located beyond 6°, the relationship between stimulus intensity and SRT was consistent with Pieron's law and other studies on SRT utilizing target contrast (Ludwig et al. 2004; White et al. 2006). Spatial target predictability also modulated SRT. Increasing the number of potential target locations first increased and then decreased SRT with decreasing spatial predictability (Fig. 3b), in apparent violation of Hick's law (Hick 1952) when 8 potential targets were presented. A positive gap effect was produced at all but the dimmest target intensities and most unpredictable spatial target predictabilities. The paradoxical effects of luminance was not accounted for by previous trial effects, error rates, or saccade accuracy error; however, the paradoxical effect of spatial target predictability from 4 to 8 targets could be accounted for by a trade-off between speed and error rate.

Effects of bottom-up target luminance on SRT

The decrease of SRT with increasing target luminance has been shown previously for oculomotor tasks (Doma and Hallett 1988; Bell et al. 2006; Boch et al. 1984; Jaskowski and Sobieralska 2004), manual response tasks (Jaskowski

and Sobieralska 2004), and general response tasks across different sensory modalities (Pieron 1952). SRT decreases have also been produced by increasing target contrast (Carpenter 2004; Ludwig et al. 2004; White et al. 2006). These previously characterized effects of decreasing response latency with increasing intensity of sensory stimuli can be explained in terms of decreased transduction, conduction, and neural processing delays. That is, as stimulus intensity or contrast increases, sensory transduction time decreases and the gain or sensitivity of the sensory response increases (Li and Basso 2008). This results in both decreased detection times and decreased SRTs. When target luminance approached detection threshold, sensory processing times increased beyond 150 ms (Fig. 5). Both physiological and psychophysical studies have provided evidence that most of this processing time occurs at the level of the retina (Barbur et al. 1998; Boch et al. 1984; Lennie 1981).

This is the first study to systematically vary target luminance from near detection threshold to supra-threshold target luminances in order to quantify: (1) the timing of the earliest stimulus-driven SRT epoch; (2) saccadic endpoint accuracy; and (3) the impact of luminance on the gap effect. Furthermore, this is also the first study to examine the relationships between luminance and parafoveal target eccentricity on SRT.

SRT increased at the brightest luminance when the target was located within an eccentricity of 6° from the fovea. When we manipulated target eccentricity, it was found that the magnitude of this paradoxical effect scaled with target distance from the fovea (Fig. 4), indicating that the effect may be related to a spatial interaction between bottom-up luminance signals in foveal and parafoveal regions. This effect has not been reported previously as relatively few laboratories utilize saccade targets that are within a few degrees of the fovea. However, in Figure 2 of a study by Palmer et al. (2007), there is a similar increase in SRT between supra-threshold target contrasts of 18 and 21% that was not mentioned in the text. Previous studies have shown increasing SRT with decreasing target eccentricity (Bell et al. 2000; Weber et al. 1992), however, the interaction of both luminance and eccentricity has never been studied systematically. The maximal paradoxical slowdown at the brightest luminances at 2° eccentricity may be related to the abolishment of express saccades that have been observed in both humans and monkeys for target eccentricities below 2° (Weber et al. 1992). As such, we hypothesize that the paradoxical U-shaped relationship between luminance and SRT should be enhanced with target eccentricities below 2° .

Neurophysiological implications

The superior colliculus (SC) and frontal eye fields (FEF) are critical structures for saccade control (Schiller et al. 1980) where these bottom-up visual and top-down saccade preparation signals have been identified on neurons carrying efferent saccadic motor commands (Hanes and Schall 1996; Wurtz and Goldberg 1972; Bruce and Goldberg 1985; Dorris and Munoz 1998; Everling and Munoz 2000; Rodgers et al. 2006). Visuomotor neurons within these structures signal both the initial afferent sensory response to the onset of a visual target as well as the efferent saccadic motor command. Recordings from these visuomotor neurons have been used to identify express and regular saccades based on the temporal separation (regular saccades) or merging (express saccades) of the visual sensory and saccadic motor bursts (Dorris et al. 1997; Edelman and Keller 1996; Sparks et al. 2000; Everling and Munoz 2000; Bell et al. 2006). Recordings from these structures will also be important to determine whether long latency express saccades can be evoked from target luminances below 1 cd/m^2 (Fig. 4). Discrepancies within previously reported ranges of express saccades across different laboratories are likely due to differences in the target luminances and/or contrasts used. Thus, express saccade ranges are not an absolute, but are instead relative to the target luminance employed (Bell et al. 2006).

Effects of top-down spatial target predictability on SRT

Hick's law (Hick 1952) states that response latency increases as a log function of the number of response alternatives. In our results, increasing the number of possible spatial target locations from 1 to 2 to 4 possible targets led to an increase in SRT in the gap task (Fig. 3b), in agreement with Hick's law. At eight possible targets, however, SRT was paradoxically decreased in both the gap and step tasks in apparent violation of Hick's law. Although the effects of spatial target predictability were consistent in the gap and step tasks individually, the effects of target predictability in the gap effect (step SRT–gap SRT) were not consistent in both animals (Fig. 6c). Thus, the apparent violation of Hick's law we observed did not appear to be related to the differences in fixation disengagement between the step and gap tasks.

Previous studies manipulated spatial target predictability but obtained inconsistent results across both human and monkey species. Some studies are consistent with Hick's law in both humans (Lee et al. 2005) and monkeys (Basso and Wurtz 1998; Thiem et al. 2008), while other studies present evidence that SRT violates Hick's law in both humans (Lawrence et al. 2008; Kveraga et al. 2002; Kveraga and Hughes 2005) and monkeys (Lawrence et al. 2008). Thus, it appears that the effect of spatial target predictability on SRT is a complex process that depends on multiple experimental variables that Hick's law alone is unable to account for universally.

Two of the studies that obeyed Hick's law, utilized cued memory tasks that required the subject to memorize 1, 2, or 4 (monkey, Thiem et al. 2008) or 1, 2, 4, or 8 (human: Lee et al. 2005) color-coded target locations. It is possible that the additional increasing demands on working memory implemented within these studies may have been the dominant factor contributing to the increase in SRT with increasing memory demands. Another monkey study which did not require memory showed that SRT also increased when up to 8 potential targets were used (Basso and Wurtz 1998) in agreement with Hick's law. This study utilized a delayed saccade task where the target location was visible before the go signal (FP disappearance) was presented.

Of the studies that presented apparent violations of Hick's law in SRT (including our study), the tasks did not require the subject to remember target locations and all the experiments involved visually guided saccades where the appearance of the target was the go signal. Kveraga et al. 2002 showed that humans performing pro-saccades supra-threshold targets *did not* change performance across spatial target predictability of 1, 2, 4 or 8 targets. Kveraga et al. 2002 concluded that "saccades made under response uncertainty must not require a time consuming process of response selection". A recent study by Lawrence et al.

(2008) showed an anti-Hick effect, whereby SRT decreased with increasing number of potential target locations in monkeys (1, 2, 4 and 8 targets) and in humans (2 and 6 targets only). Lawrence et al. hypothesized that the inhibition required to prevent premature saccades contributed to their results such that this inhibition increased with increasing target certainty. Lawrence et al.'s result partially agrees with our data as we observed a decrease in SRT from 4 to 8 potential targets.

We hypothesize that this paradoxical latency increase with eight possible targets can be accounted for by the spatial interactions of the top-down spatial target predictability signal within critical structures of the oculomotor system. The local excitation and distal inhibition hypothesized to exist within the spatial SC map (Trappenberg et al. 2001) leads to inhibitory competition when spatially separate locations within the map are activated. Evidence for this 'Mexican hat' like spatial response, has also been demonstrated previously in the visual responses of FEF neurons during visual search in which a saccade target is presented within a circular array of distracters (Schall et al. 1995). These FEF neurons showed distracter related inhibition of the visual response that extended beyond 30° of visual angle from the target (Schall et al. 1995). Because of this local excitation and distal inhibition relationship within the saccadic system, we hypothesize that the top-down signals coding the potential target locations in our task would inhibit each other when fewer spatially distinct locations were activated, thus increasing SRT with increasing potential target locations. When the potential target locations become too numerous, such as the case when we increased the total number of potential targets from 4 to 8 (or when Lawrence et al. 2008 increased from 2 to 6), the distinct spatial top-down activity could merge and result in global excitation which reduced SRT. The SC is an excellent candidate where these spatial target interactions may occur as it contains a retinotopic topographic sensory-motor map for saccades. Furthermore, the spatial visual and saccadic receptive fields in the SC (around 6° eccentricities) have been shown to encompass up to several hundred square degrees of the visual field (Marino et al. 2008).

One important methodological difference between the earlier studies and our study is that all of these previous studies (with the exception of a single control experiment by Lawrence et al. 2008) utilized continuously visible target placeholders. We hypothesize that our observed decrease in SRT from 4 to 8 targets may have resulted from the lack of visible placeholders, which resulted in internal top-down prediction mechanisms exceeding their built-in capacities. By not trying to predict target locations when there were eight possible targets, the monkeys likely changed their strategy to be completely driven by bottom-up sensory information. It is also possible that because the

number of possible target locations changed daily, there may be idiosyncratic order effects contributing to this finding as the eight-target condition was performed on different days than the 1, 2 and 4 target conditions. These potential order effects should have been minimized if not eliminated; however, as they were counterbalanced by ensuring that each target predictability condition was repeated across multiple daily sessions.

The effects of luminance, prediction, and fixation offset in the gap effect

SRTs were decreased in the gap task relative to the step task in both monkeys across all conditions except the dimmest target luminance of 0.001 cd/m². This contradicts a previous human study which did not show any difference in the magnitude of the gap effect between target luminances of 0.4 and 40 cd/m² (Reuter-Lorenz et al. 1991). We hypothesize that this previous study may not have observed a change in the gap effect due to the dim FP used (0.8 cd/m²). Because our study utilized a brighter FP (3.5 cd/m²), the disinhibitory effects of the FP offset during the gap would be greater and could have interacted more strongly with target luminance. Future studies of the gap effect should explore a manipulation of FP luminance in order to provide more insight into this issue. Finally, as the Reuter-Lorenz et al. (1991) study utilized humans and not monkeys, a species difference may have resulted in the discrepancies between our study and theirs.

The reduced gap effect we observed at the dimmest luminance indicates that target detection time for near detection threshold stimuli overshadows any benefits potentially afforded by the gap. Thus, the gap task only yielded a behavioral advantage when target detection times were rapid.

Predictability involves anticipatory information that has been gained from experience learned in previous trials. Once learned, this prediction signal is available to influence incoming sensory signals in order to improve reaction time performance. This experience can be made available to the saccadic system for subsequent trials (Basso and Wurtz 1997). Neurophysiological recordings from neurons in the SC have identified pre-target activity during the gap period that is correlated with SRT (Dorris and Munoz 1995, 1998; Dorris et al. 1997; Dias and Bruce 1994; Everling and Munoz 2000). It has been asserted that the gap causes saccade-related neurons in these oculomotor structures to increase their level of excitability such that they are closer to some theoretical saccade trigger threshold before the bottom-up visual target signal arrives (Munoz et al. 2000). However, it has also been shown that these pre-target increases in neural activation during the gap also scale with spatial target predictability in the SC (Basso and Wurtz

1997; Basso and Wurtz 1998; Dorris and Munoz 1998). This evidence indicates that the increase in activity during the gap is likely related to top-down spatial and possible temporal predictability (in addition to bottom-up fixation point disappearance) which results in saccades that can be triggered faster from a relatively smaller increase in activation (Dorris and Munoz 1998).

Behaviorally, the gap effect modulated SRT more than spatial predictability in our study. Because of the very short 200-ms duration of the gap period, it is unlikely that the limited top-down temporal predictability in the gap was affecting SRT more strongly than spatial predictability. A more likely hypothesis is that the gap effect was primarily influenced by bottom-up fixation offset effects. Fixation point disappearance alone has been shown to decrease SRT by eliminating the inhibition that results from active visual fixation (Dorris and Munoz 1995; Krauzlis 2003; Machado and Rafal 2000; Pare and Munoz 1996). Thus, we hypothesize that the magnitude of the gap effect is primarily driven by the bottom-up disappearance of the fixation point. Because of this interaction between top-down and bottom-up factors in the gap, an independent analysis of the individual bottom-up and top-down contributions will require further study.

Thus, understanding the individual relative behavioral influences of temporal and spatial prediction requires a different kind of task that could dissociate the top-down temporal prediction component of the gap effect from the bottom-up fixation offset component. Physiologically it will be important to dissociate what component of the increase in baseline activation of SC and FEF visual and saccade neurons is related to top-down spatial and temporal prediction and which component is driven by bottom-up fixation offset effects.

Conclusions

Top-down and bottom-up factors significantly affect the neural processing times underlying SRT. Modulating target luminance affected detection times and significantly impacted overall SRT. The relationship between target luminance and SRT was U-shaped and violated Pieron's law. The magnitude of the gap effect was significantly impacted by target luminance, indicating that bottom-up properties of the visual stimulus are important for the optimization of specific top-down behavioral effects. Top-down spatial predictability also significantly influenced SRT; these differences may be governed by the limitations of attention and memory.

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