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Spatial attention during saccade decisions

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Jonikaitis D, Klapetek A, Deubel H. Spatial attention during saccade decisions. *J Neurophysiol* 118: 149–160, 2017. First published March 29, 2017; doi:10.1152/jn.00665.2016.—Behavioral measures of decision making are usually limited to observations of decision outcomes. In the present study, we made use of the fact that oculomotor and sensory selection are closely linked to track oculomotor decision making before oculomotor responses are made. We asked participants to make a saccadic eye movement to one of two memorized target locations and observed that visual sensitivity increased at both the chosen and the nonchosen saccade target locations, with a clear bias toward the chosen target. The time course of changes in visual sensitivity was related to saccadic latency, with the competition between the chosen and nonchosen targets resolved faster before short-latency saccades. On error trials, we observed an increased competition between the chosen and nonchosen targets. Moreover, oculomotor selection and visual sensitivity were influenced by top-down and bottom-up factors as well as by selection history and predicted the direction of saccades. Our findings demonstrate that saccade decisions have direct visual consequences and show that decision making can be traced in the human oculomotor system well before choices are made. Our results also indicate a strong association between decision making, saccade target selection, and visual sensitivity.

NEW & NOTEWORTHY We show that saccadic decisions can be tracked by measuring spatial attention. Spatial attention is allocated in parallel to the two competing saccade targets, and the time course of spatial attention differs for fast-slow and for correct-erroneous decisions. Saccade decisions take the form of a competition between potential saccade goals, which is associated with spatial attention allocation to those locations.

decision making; saccades; spatial attention; working memory

DESPITE THE FACT that we, seemingly automatically, move our eyes several times per second, each of our saccades has to be preceded by some decision-making process, in which the saccade goal is selected among other possible goals. Whereas traditional theories of decision making postulated that decisions are first made by cognitive systems and only then implemented in the form of motor actions, recent neurophysiological findings challenge these serial models by supporting the view that motor decisions consist of a biased competition between alternative motor plans that are represented in parallel

in sensorimotor brain areas (Andersen and Cui 2009; Cisek 2007; Cisek and Kalaska 2010).

Computational models of the decision process assume that sensory evidence in favor of each movement alternative is integrated over time and gradually accumulated toward a threshold, at which the corresponding action is initiated (Brown and Heathcote 2008; Carpenter and Williams 1995; Ratcliff and McKoon 2008). The starting point, or baseline, of the accumulation depends on the prior probability that the given movement will be executed (Carpenter and Williams 1995), whereas the rate of accumulation depends on the strength of the sensory evidence and other variables, such as the value associated with the given response (Gold and Shadlen 2007).

Numerous nonhuman primate neurophysiology studies have supported these assumptions by showing that the outcome of saccadic decisions directly depends on sensory information (Newsome et al. 1989; Salzman et al. 1990) and that this decision-related sensory evidence is accumulated in visuomotor brain areas, such as lateral intraparietal cortex (LIP) (Gold and Shadlen 2000; Ipata et al. 2006; Roitman and Shadlen 2002; Shadlen and Newsome 1996, 2001), frontal eye field (Hanes and Schall 1996; Kim and Shadlen 1999; Schall 2003), and superior colliculus (SC) (Glimcher and Sparks 1992; Munoz and Wurtz, 1995; Sparks 1978; Wurtz and Goldberg 1972). A functional MRI (fMRI) study in humans, in which two eye movements had to be planned in sequence, also provided evidence that the posterior parietal cortex (containing the human homolog of LIP) represents goals of upcoming saccades (Medendorp et al. 2006).

When nonhuman primates have to decide between two saccade targets, neurons in visuomotor brain areas represent both response alternatives, with a stronger signal corresponding to the selected goal (Kim and Basso 2008; Platt and Glimcher 1997), and the representations are modulated by the perceived probability or value of the responses (Basso and Wurtz 1998; Sugrue et al. 2004). Consistent with this, behavioral studies show that competitive visual environments not seldom lead to the parallel programming of two, or possibly even more, saccades (Becker and Jürgens 1979; Godijn and Theeuwes 2002; Irwin et al. 2000; Klapetek et al. 2016; Massen 2004; McPeck et al. 2000; Morrison 1984; Theeuwes et al. 1999; Walker and McSorley 2006).

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Unfortunately, many of the studies that demonstrated decision-related neural activity investigated saccades to visual targets, which makes it difficult to judge whether the neural signals reflected perceptual decision making or saccade planning. A possible way to distinguish between the two processes is to dissociate visual information and saccade planning spatially (as, for example, in the antisaccade task, where saccades have to be directed away from a visual stimulus) or temporally (by presenting the saccade cue after the disappearance of the visual information). A few studies reported activity of LIP neurons while nonhuman primates performed antisaccades (Gottlieb and Goldberg 1999; Zhang and Barash 2000, 2004), their results being contradictory. Whereas Gottlieb and Goldberg (1999) found that only a few LIP neurons represented purely saccade-related activity and most cells showed visual responses, Zhang and Barash (2000, 2004) observed that most neurons could carry visual as well as motor activity, depending on the context.

To investigate saccade decisions in humans, one can take advantage of the tight coupling between oculomotor and perceptual selection. During saccade preparation, perception is enhanced at the saccade target (Deubel and Schneider 1996; Hoffman and Subramaniam 1995; Jonikaitis and Deubel 2011; Jonikaitis and Theeuwes 2013; Klapetek et al. 2016; Kowler et al. 1995; Puntiroli et al. 2015; Rolfs et al. 2011). On the other hand, the presentation of salient perceptual events, such as irrelevant distractors, often leads to involuntary saccades in the direction of these stimuli, which has been termed oculomotor capture (Theeuwes et al. 1999, 2011). Such observations (Ptak 2012) corroborate the hypothesis that oculomotor and visual selection are coupled through a common attentional priority mechanism, which selects behaviorally most relevant location (Fecteau and Munoz 2006; Serences and Yantis 2006). If this is true, we should expect that any saccade decision (reflected in accumulation of evidence in favor of a particular location on the priority map) should also be reflected in gradually improving perceptual performance at the corresponding spatial location.

To test this hypothesis, we designed an experiment in which human observers had to choose between two memorized saccade targets (either freely or on the basis of a color rule) and simultaneously discriminate visual probes at the two competing target locations or elsewhere in the display. By probing discrimination performance at variable times during the trial, we were able to measure the time course of the perceptual selection of both target locations. Consistent with the previously reviewed evidence on the coupling between saccadic and perceptual selection, we expected to see a clear perceptual benefit at the chosen target. We were also interested in whether a perceptual benefit would be evident at the competing (non-chosen) target location as well. It is possible that both saccade targets (or the oculomotor programs toward them) are simultaneously represented in visuomotor brain areas and facilitate perception at both corresponding spatial locations. A second possibility, however, is that the nonchosen target is treated as an irrelevant distractor and can be ignored or even inhibited from early on. A third possibility is that the pattern of perceptual facilitation would differ in the rule-based and in the free-choice conditions, for example, due to smaller competition of the nonchosen target in the rule-based condition than in the free-choice condition.

METHODS

We report how we determined our sample size, as well as all data exclusions, data manipulations, and measures in this study. Our experimental data and code are freely available at <https://zenodo.org> under the following DOI: 105281/zenodo.268029.

Participants

Twelve observers (age 21–29 yr, 7 women) completed the experiment for payment. All participants were naive as to the predictions of the study. The experiments were carried out with the approval of the department's ethic committee and in accordance with the Declaration of Helsinki, and all participants gave written informed consent.

Participant Selection and Data Collection

We observed a clear pattern of experimental results at the individual participant level for the first 5 participants and decided to fix the size of the final data set to 12 participants. Two participants were not able to discriminate perceptual probes and did not complete the data collection.

Apparatus

The observers were seated in a quiet and dimly illuminated room in front of a gamma-linearized 21-in. CRT monitor (SONY GDM-F500R, 1,024 × 768 pixels, 120 Hz), positioned at a viewing distance of 60 cm. Right-eye gaze position was recorded with an EyeLink 1000 desktop-mounted eye tracker (SR Research, Kanata, ON, Canada) at a sampling rate of 1,000 Hz while head movements were minimized through the use of a chin and forehead rest. The eye tracker was calibrated before each new block and whenever it was necessary. Stimulus presentation and response collection were controlled by an Apple Mac Mini, using MATLAB software (The MathWorks, Natick, MA) and the Psychophysics and EyeLink Toolbox extensions (Brainard 1997; Cornelissen et al. 2002; Pelli 1997). Manual responses were collected via the arrow keys on the right-hand side of the computer keyboard.

Procedure

Main task. Figure 1 illustrates the visual displays and stimulus timing. Each trial started with a fixation target (black dot, diameter 0.75° of visual angle) presented on a gray background. Five square objects (diameter 2.8°) were positioned on an imaginary circle around fixation (radius 7°); the angular position of the first object was 30° plus a random jitter between -10 and 10°, and the angular distance between objects was 72°. Each square object consisted of an alternating stream of vertically oriented Gabor patches (spatial frequency: 2.5 cycles per degree, 100% contrast, random phase selected on each presentation) and grayscale noise masks [pixel luminance values randomly drawn from a Gaussian distribution with minimum 0 (black) and maximum 255 (white), mean = 128 and SD = 128]. Gabor patches and noise masks alternated every four display refresh frames (33 ms, or in some cases 40 ms).

During an initial memory cue phase (Gaussian distribution with mean = 2,000 ms and SD = 100 ms), two of the streams were highlighted by color frames (one blue and the other green) and participants were asked to memorize their locations. The memory cue phase was followed by a delay of 500 to 1,500 ms (duration selected randomly from a uniform distribution), during which the colored frames were extinguished. After the delay, a central saccade cue was presented for 700 ms: the fixation target changed color to a blue, green, or orange (all 3 colors were equiluminant) with equal probability. A green or blue fixation instructed a saccade to the corresponding memorized green or blue target location (rule-based choice),

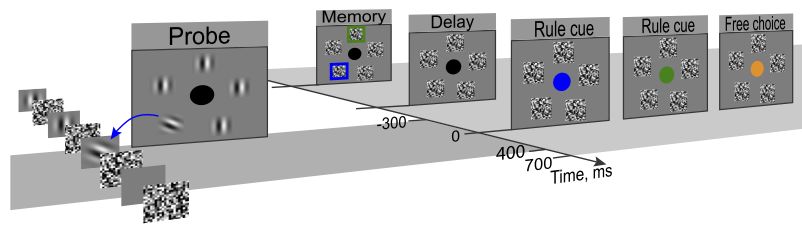


Fig. 1. *A*: schematic depiction of the sequence of stimuli. During the memory cue period, 2 colored frames indicated the memory target locations. After a delay, the saccade cue was presented. The saccade cue was a color change of the fixation: blue (1/3 of trials) or green (1/3 of trials) indicated that participants had to make a saccade toward the previously presented blue or green target (rule-based choice), whereas orange (1/3 of trials) indicated that either of the 2 targets could be selected (free choice). During the entire trial, each of the 5 locations contained a rapidly alternating stream of white noise masks and vertically oriented Gabor patches. A probe was presented in one of the locations. The probe was a briefly shown tilt of one of the Gabors clockwise or counterclockwise from the vertical. The probe appeared between -300 and 400 ms relative to the onset of the saccade cue. An example probe stream is shown in the *inset*.

whereas an orange fixation indicated a saccade to either of the two memorized locations (free choice). After 700 ms, the fixation and all square objects were removed.

A probe display was presented -300 to 400 ms relative to saccade cue onset (time selected randomly from a uniform distribution). The probe was a Gabor patch tilted clockwise or counterclockwise (angle of tilt determined for each participant; see *Threshold task* below) and was presented for four frames (33 ms, or in some cases 40 ms) in one of the five object streams (selected randomly with equal probability).

After probe offset, no Gabor patches were further shown, so the object streams consisted of alternating noise masks and blank sequences. Observers reported the perceived probe orientation by pressing the left (counterclockwise tilt) or right (clockwise tilt) arrow key. We instructed observers to focus on making fast and accurate saccades and to guess whenever they were unsure about the probe orientation. Discrimination responses were not speeded. A new trial started 200 ms after the discrimination response.

Observers participated in 14 – 25 main task sessions (depending on their availability), with each session consisting of 400 trials. They usually performed one or two 1-h sessions on a single day.

Threshold task. We determined the probe tilt angle for each participant at the beginning of each recording day. The visual stimuli in the pretest were identical to those in the main task, except that only one memory target was presented, and it always predicted the location of the probe (100% valid cue).

Observers were instructed to covertly attend to the memory target while maintaining central fixation and to report the orientation of the probe. The tilt angle at which observers reached 80% correct probe discrimination was determined using a modified version of the QUEST staircase procedure (King-Smith et al. 1994; Watson and Pelli 1983) implemented in the MATLAB Psychophysics toolbox.

Data Analyses

Drift correction was performed offline using the average gaze direction (given that no saccades of amplitude larger than 0.5° occurred) between 100 and 10 ms before memory delay onset. Saccades were detected offline using an algorithm that evaluated eye velocity changes (Engbert and Mergenthaler 2006): if eye velocity exceeded its average velocity on a given trial by 6 SD and for more than 6 ms, a saccade onset was detected. We classified saccades as correct if the saccade starting point was less than 2° away from fixation, the endpoint was less than 3° away from the target center, and the onset latency was between 50 and 700 ms. We removed trials due to breaking of fixation if a saccade larger than 2° occurred during the last 200 ms before saccade cue onset (anticipatory saccades) or between cue onset and correct saccade initiation (erroneous saccade before the onset of the correct saccade). Trials were also removed if blinks occurred in the interval starting 100 ms before saccade cue onset and ending with saccade onset. On trials where the two target locations were adjacent (angular distance 72°), the saccade was classified as either correct or incorrect, depending on whether the first

saccade landed closer to the cued or the noncued location. Data from each participant were inspected manually for saccade and microsaccade detection accuracy and data recording noise. In total, participants selected the correct target on $80,128$ and the erroneous target on $14,908$ of the total $102,451$ recorded trials (7% of trials had to be removed for reasons mentioned above).

We computed differences between the means for each participant and then computed two-tailed P values from the bootstrapped population distribution of these differences. Bootstrapped distributions were calculated by drawing with replacement $10,000$ bootstrap samples from each condition's data set.

RESULTS

Properties of Saccades

Response latency and accuracy are the two main measures of the outcome of any decision making process. Further measures of motor performance, such as trajectory deviations, also have been used as a basis for inferences about competitive processes underlying choices between multiple motor plans (Chapman et al. 2010; McSorley and McCloy 2009; Song and Nakayama 2008; Welsh and Elliott 2004).

Figure 2*A* shows the distributions of saccade latencies. Latencies (means \pm SE) were slightly shorter in the free-choice condition (234 ± 8 ms) than in the rule-based condition (241 ± 7 ms, $P = 0.003$). A comparison of saccade latencies on correct and error trials in the rule-based condition (note that decision errors could not occur in the free-choice condition)

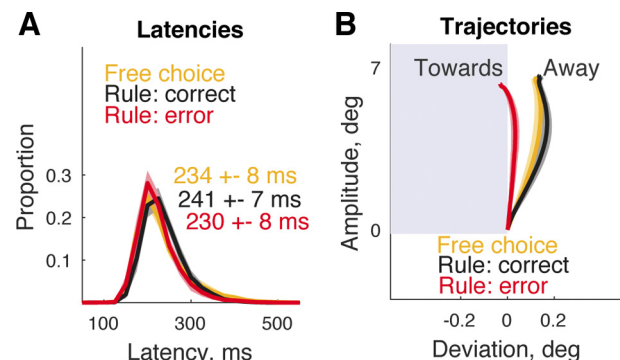


Fig. 2. *A*: saccade latency distributions in the free and rule-based choice tasks. Errors were defined as wrong saccade target selection during the rule-based condition. Shaded areas represent SE. *B*: saccade trajectories toward or away from the nonchosen target. Locations were rotated and flipped so that all nonchosen targets appear to the left of the saccade goal in the figure. Saccade trajectories toward the nonchosen target fall on the shaded background area, whereas trajectories away from it fall on the white background area.

revealed shorter latencies on error trials (230 ± 8 ms) than on correct trials (241 ± 7 ms, $P < 0.001$).

Figure 2B shows the saccade trajectories. In human studies, saccade trajectories tend to deviate away from competing stimuli if they are successfully suppressed on the motor map of the SC, and toward distractors if this suppression fails (Sheliga et al. 1995; Van der Stigchel et al. 2006).

We observed that saccade trajectories deviated away from the nonchosen target both in the free-choice and in the rule-based conditions. Surprisingly, this deviation away was abolished on error trials. Saccade deviation on error trials ($0.03 \pm 0.03^\circ$) was smaller than on both correct rule-based trials ($0.30 \pm 0.03^\circ$, $P < 0.001$) and on free-choice trials ($0.26 \pm 0.05^\circ$, $P < 0.001$). This suggests that suppression of the nonchosen target was reduced on error trials. However, two different reasons could underlie this reduced suppression. First, it is possible that both targets were represented in the oculomotor system and that the representation of the nonchosen target was not suppressed. Second, only the erroneously chosen saccade target may have been represented on error trials, and the correct target may simply not have been considered from the beginning. Neither alternative can be ruled out, because motor responses only reflect the final state of competition between possible movement targets, shortly before or during movement execution.

Unfortunately, the latency and trajectory differences observed in our study represent only the final state of motor decisions and thus limit conclusions on the decision-making process itself. We will therefore focus on attention allocation during decision making, which will allow us to track the decision-making process before motor responses.

Attentional Selection

On the basis of the existing literature, we expected to find 1) that attention would be maintained at the locations held in working memory during the delay interval and 2) that attention would shift to the saccade goal before saccade onset. To measure attention allocation during the memory delay, we calculated visual sensitivity (d -prime) in the probe discrimination task at each probe location in the range 300–200 ms before the onset of the saccade cue. Visual sensitivity (mean \pm SE) was superior at both memorized locations. Compared with the average value of the three task-irrelevant locations (0.1 ± 0.1), d -prime values were higher at the location of the green (1.0 ± 0.2 , $P < 0.001$) and the blue memory targets (1.1 ± 0.2 , $P < 0.001$). This indicates that both locations were selected by visuospatial attention, possibly to strengthen their representation in working memory by spatial rehearsal (Awh and Jonides 2001).

Next, we focused on discrimination performance after the appearance of the saccade cue. In line with earlier studies on saccade preparation and spatial attention (Born et al. 2012; Deubel and Schneider 1996; Godijn and Theeuwes 2003; Hoffman and Subramaniam 1995; Jonikaitis and Deubel 2011; Jonikaitis and Theeuwes 2013; Klapetek et al., 2016; Kowler et al. 1995; Puntiroli et al. 2015; Rolfs et al. 2011), we found that saccade preparation was associated with improved target discrimination at the future saccade goal. Visual sensitivity (100–0 ms before saccade onset) was higher at the chosen target (3.2 ± 0.3) than at the nonchosen target (1.5 ± 0.2 , $P <$

0.001), as well as at irrelevant locations (0.3 ± 0.1 , $P < 0.001$). Taking these findings together, the pattern of perceptual discrimination performance suggests that spatial attention shifted to the saccade goal whenever a saccade was prepared.

Attentional Selection is Linked to Decision Making

Figure 3 shows the spatiotemporal distribution of the pre-saccadic visual sensitivity during decision making. An increase in sensitivity occurred at both competing target locations, whereas there was little to no sensitivity increase at the irrelevant locations. Furthermore, sensitivity at the nonchosen location increased regardless of whether it was close to the chosen target (angular distance 72°) or farther away from it (angular distance 144°), with no benefit at the location between the chosen and nonchosen target locations in the latter case (Fig. 3D). This indicates that target selection is spatially specific to chosen and nonchosen target locations.

To evaluate whether spatial attention reflects the process of saccadic decision making, we measured how visual sensitivity after saccade cue onset changed relative to visual sensitivity during the memory delay. For this purpose, we first calculated a visual sensitivity baseline by determining the average sensitivity during the memory delay (-300 to -150 ms before the saccade cue) separately for the chosen, nonchosen, and task-irrelevant locations, as well as for each choice condition. Next, we calculated the time course of the visual sensitivity for the chosen, nonchosen, and task-irrelevant locations and sub-

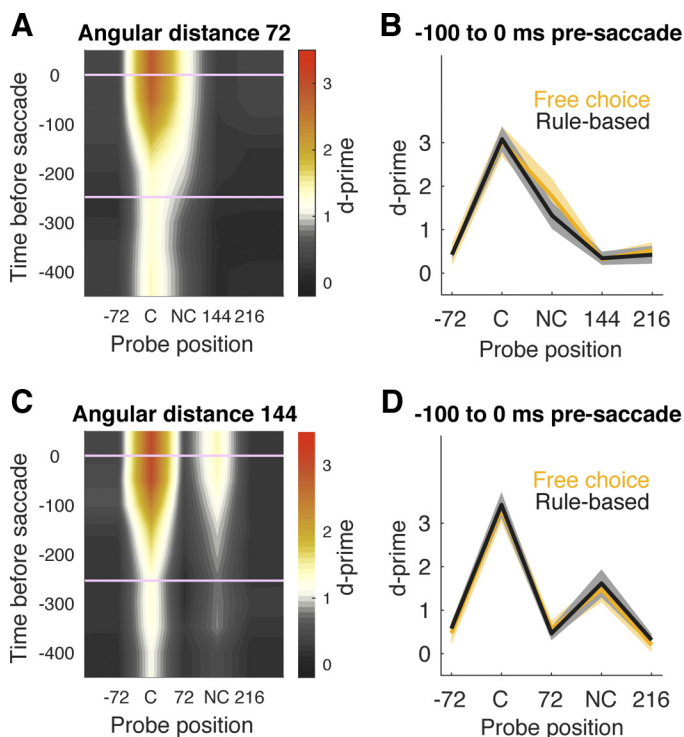


Fig. 3. Attention allocation in the decision task. *A*: visual sensitivity before saccade onset at all 5 measured locations. Memorized target locations are labeled C (chosen target) and NC (nonchosen target). Angular distance between both targets was 72° . *B*: visual sensitivity before saccade onset. Radial distance between both targets was 72° . *C*: visual sensitivity before saccade onset at all 5 measured locations. Radial distance between both targets was 144° . *D*: visual sensitivity in the free-choice and rule-based conditions between 100 and 0 ms before saccade onset. Radial distance between both targets was 144° . Shaded areas represent SE.

tracted the baseline visual sensitivity from this time course. We hence obtained a measure of how visual sensitivity at the chosen, nonchosen, and task-irrelevant locations increased or decreased compared with the sensitivity during the memory delay. Figure 4, *A* and *B*, shows this change in visual sensitivity in the rule-based and free-choice conditions over time. Visual sensitivity is shown relative to saccade cue onset and relative to saccade onset. After cue onset, sensitivity increased at both the chosen and the nonchosen targets. During rule-based decisions, the visual sensitivity increase (d -prime values 100 to 0 ms before saccade onset) was larger at the chosen target (1.9 ± 0.1) than at irrelevant locations (0.2 ± 0.1 , $P < 0.001$), and this benefit was also present at the nonchosen target (0.8 ± 0.1 , $P < 0.001$). Comparable results were observed during the free-choice task (chosen target: 1.7 ± 0.2 vs. irrelevant: 0.1 ± 0.1 , $P < 0.001$; nonchosen target: 0.8 ± 0.2 vs. irrelevant, $P < 0.001$). Figure 4, *C* and *D*, shows the change in visual sensitivity for individual participants. For all participants, visual sensitivity before saccade onset increased at both the chosen and the nonchosen targets (-100 to 0 ms; *insets* in Fig. 4, *C* and *D*). These results show that both target locations were consistently selected by attention during the decision-making period.

So far, our results support the following conclusions: First, oculomotor decisions involve the allocation of spatial attention to potential saccade targets. This allowed us to track decision making before motor effects of decisions (such as saccadic latency or curvature) became observable. The attention allocation is clearly related to the decision process, because it occurred in the absence of visual information. Second, attention remains allocated to both potential saccade goals until the onset of the saccade. Surprisingly, we observed this in the

rule-based choice condition, where the saccade target was defined by a simple stimulus-response mapping.

Attentional Selection is Associated with Saccade Onset

We next investigated whether the observed attentional selection was directly associated with saccade responses. For this purpose, we examined the relationship between saccade latencies and the time course of visual sensitivity (Fig. 5). If covert attention indeed reflects decision making, then faster decisions, as indicated by shorter saccade latencies, should be preceded by earlier attentional selection. In this context, two factors can influence the speed of decisions. One is the rate at which sensory evidence is accumulated toward the decision boundary, and the other is the starting point of the accumulation.

To compare trials with faster and slower saccades, we separated saccade latencies at the median for each participant (short latencies were on average 217 ms, and long latencies were 269 ms). First, we focused on visual sensitivity at the chosen target location. As can be seen in Fig. 5*A*, we observed that after the onset of the saccade cue visual sensitivity increased earlier before faster saccadic responses and improved later before slower saccadic responses. Visual sensitivity at the chosen target location (100–200 ms after saccade cue onset) was better during short-latency trials (2.9 ± 0.3) than during long-latency trials (2.1 ± 0.2 , $P < 0.001$). The *inset* in Fig. 5*A* shows that the distribution of individual visual sensitivity differences was shifted toward positive values (100–200 ms after saccade cue onset) at the chosen target location. Figure 5*B* shows the time course difference of the visual sensitivity (long – short latency). Visual sensitivity at the chosen target location around cue onset was slightly higher for short-latency saccades, and this difference rapidly increased during saccade

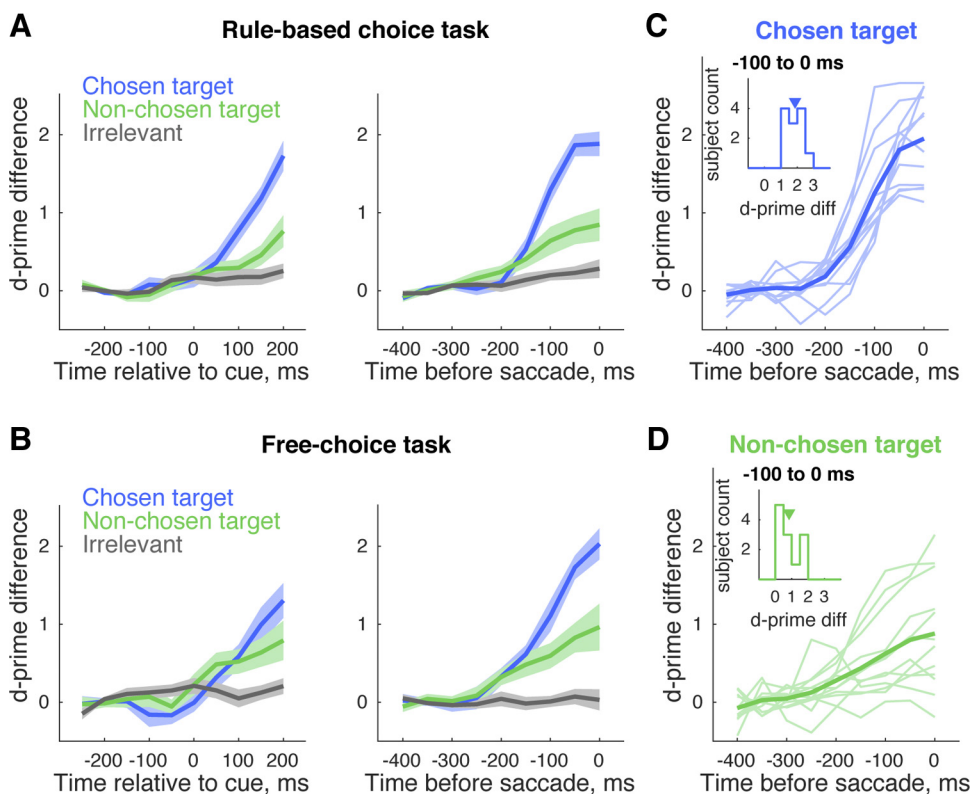


Fig. 4. Attentional selection during decision making. *A*: time course of the visual sensitivity difference in the rule-based condition. The difference (in d -prime) was calculated by subtracting the visual sensitivity during the memory delay (300–150 ms before saccade cue onset) from the time course of visual sensitivity relative to cue or saccade onset. *B*: time course of the visual sensitivity difference in the free-choice condition. *C*: time course of the visual sensitivity difference for individual subjects at the chosen target. Thin lines represent individual subjects; thick line indicates the sample mean. *D*: time course of the visual sensitivity difference for individual subjects at the non-chosen target location. *Insets* (*C* and *D*) show histograms of the visual sensitivity difference (d -prime diff) 100–0 ms before saccade onset.

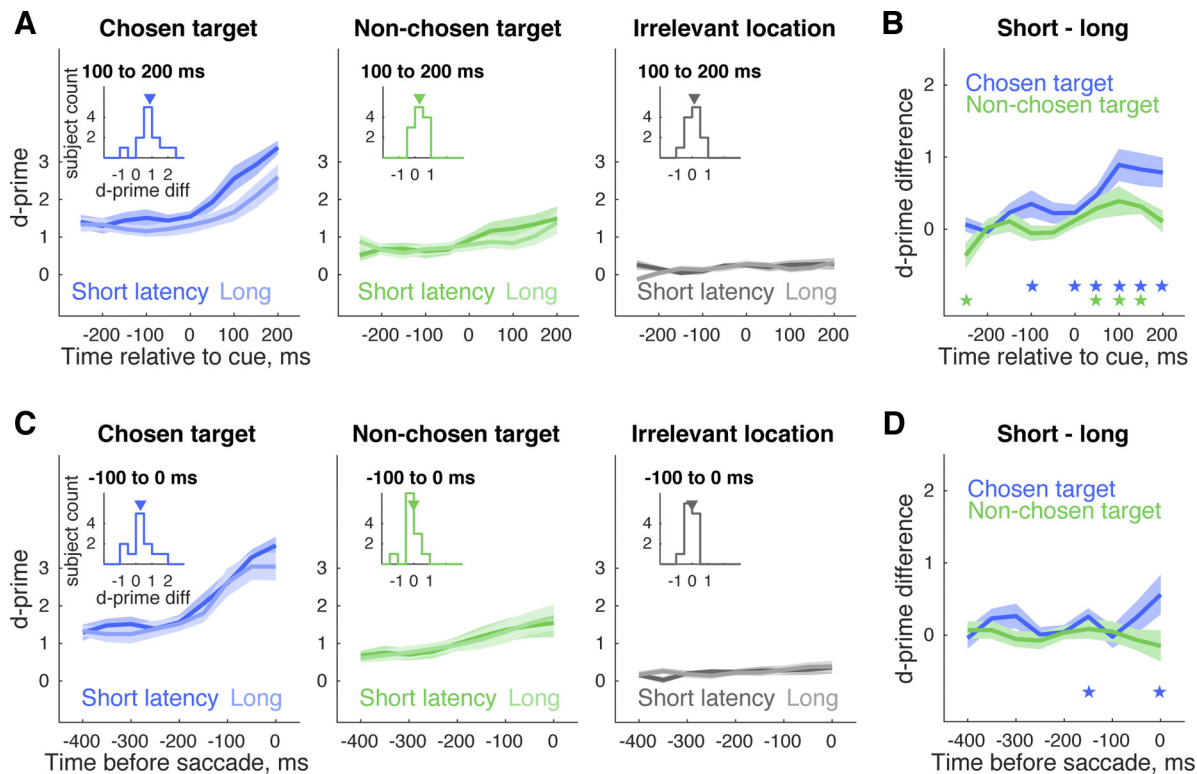


Fig. 5. Attentional selection before saccades with short and long latencies. *A*: visual sensitivity at the chosen target, nonchosen target, and at irrelevant locations relative to saccade cue onset. *Insets* (*A* and *C*) show histograms of the visual sensitivity difference (*d*-prime diff) between trials with short and with longer saccade latency 100–200 ms after saccade cue onset. *B*: difference in visual sensitivity at chosen and nonchosen targets between trials with short and long saccade latency, plotted relative to saccade cue onset. Bootstrap comparisons between 2 conditions: * $P < 0.05$ for a given time bin. *C*: visual sensitivity at the chosen target, nonchosen target, or an irrelevant location relative to saccade onset. *D*: difference in visual sensitivity at chosen and nonchosen targets between trials with short and with long saccade latency, plotted relative to saccade onset.

preparation. Figure 5, *C* and *D*, replots visual sensitivity relative to saccade onset. We observed a comparable increase in visual sensitivity for fast and slow decisions at the chosen target location. Visual sensitivity in the interval 100–0 ms before saccade onset was comparable for short-latency trials (3.3 ± 0.3) and long-latency trials (3.0 ± 0.4 , $P = 0.25$). These findings (at the group level) are compatible with the assumption that faster and slower decisions differ mainly in the starting point of the accumulation of sensory evidence.

Figure 5, *A* and *B*, additionally shows that latency differences were also associated with differences in discrimination performance at the nonchosen target. Visual sensitivity at the nonchosen target 100–200 ms after saccade cue onset was higher before short-latency saccades (1.3 ± 0.3) than before long-latency saccades (1.0 ± 0.2 , $P = 0.001$), which suggests that the attention shift to the nonselected target was also linked to saccade onset. The *inset* in Fig. 5*A* shows that the distribution of individual visual sensitivity indexes was shifted toward positive values (100–200 ms after saccade cue onset). Figure 5*B* shows the time course difference of the visual sensitivity (long – short latency). Visual sensitivity at the nonchosen target location was higher during the preparation of short-latency saccades compared with long-latency saccades, even though the saccade was never directed to the nonchosen target. Finally, Fig. 5, *C* and *D*, shows that visual sensitivity in the interval 100–0 ms before saccade onset was comparable for short-latency trials (1.5 ± 0.3) and long-latency trials (1.5 ± 0.4 , $P = 0.61$).

Our results thus demonstrate that the timing of the attentional selection of the competing saccade targets is related to the timing of the saccade decision. An apparent interpretation is that participants were simply more alert on short latency trials, which could lead to both an earlier increase in discrimination performance and to faster saccade programming. This explanation is unlikely, however, because discrimination performance at the irrelevant locations was not modulated by saccade latency (Fig. 5, *A* and *C*). Visual sensitivity at the irrelevant locations (100–200 ms after saccade cue onset) did not differ between short-latency saccades (0.3 ± 0.1) and long-latency saccades (0.2 ± 0.1 , $P = 0.5$). The effect of saccade latency on discrimination performance was instead restricted to the decision-relevant locations, suggesting that a spatially specific competition between these two locations had taken place.

Choice Errors Are Related to Attentional Biases

We observed that in the rule-based choice condition participants correctly selected the instructed target on 78% of the trials and made an erroneous selection on 22%. Given the size of our data set, we recorded on average ~1,200 error trials per participant, which allowed us to perform an analysis of attentional selection during error trials. Our results on saccade trajectory deviations (Fig. 2*B*) permitted two opposing hypotheses: either the nonchosen location was not suppressed, or it was not represented from the beginning.

Figure 6*A* compares visual sensitivity at the chosen target on correct and on error trials. It is evident that the target was

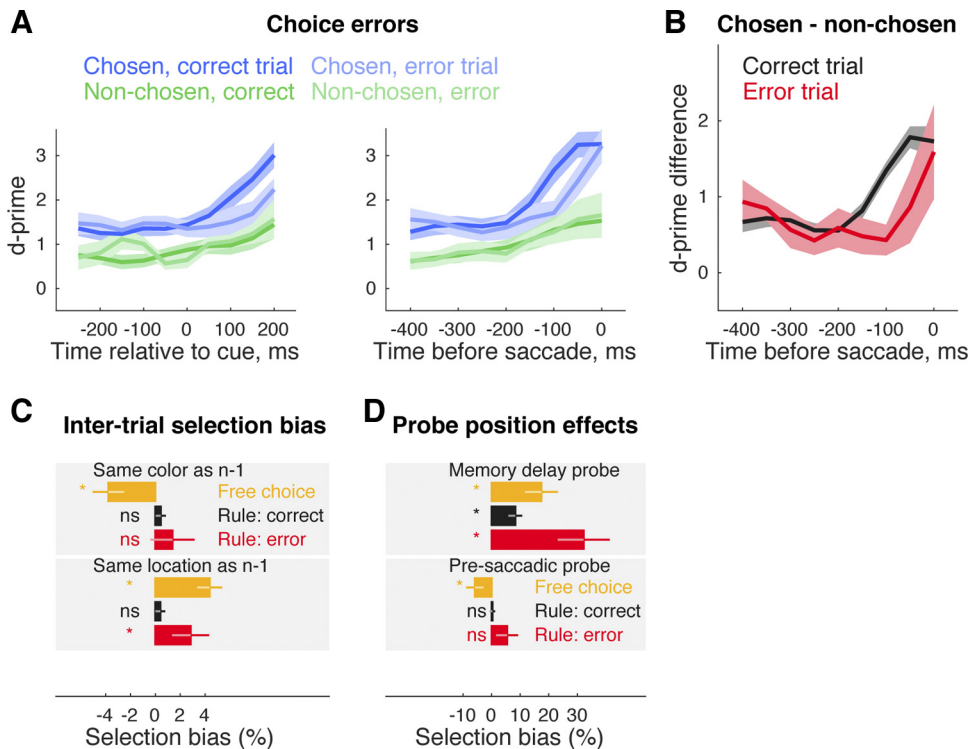


Fig. 6. Error trials. *A*: visual sensitivity during rule-based decisions relative to cue onset or relative to saccade onset. *B*: difference in visual sensitivity between the chosen and nonchosen target on correct and on error trials. *C*: saccade choice as a function of previous choice. Selection bias is defined as the percentage of trials on which participants were more likely (positive bias) or less likely (negative bias) to choose a target of the same color (*top*) or same location (*bottom*) as in the preceding trial. Error bars represent SE. Bootstrap comparisons between 2 conditions: * $P < 0.05$; ns indicates $P \geq 0.05$. *D*: target location as a function of probe location. Selection bias is defined as the percentage of trials on which participants were more likely or less likely to choose the target at the same location as a probe presented during the memory delay period (*top*) or as a probe presented after the saccade cue (*bottom*).

selected later on error trials than on correct trials. Because of this, visual sensitivity (100–200 ms after saccade cue onset) was better at correctly chosen targets (2.5 ± 0.3) than at erroneously chosen targets (1.7 ± 0.3 , $P = 0.003$). However, discrimination performance at the nonchosen target also improved before saccade onset, indicating that both targets still competed on error trials. Indeed, discrimination performance at the nonchosen target (100–200 ms after saccade cue onset) was comparable on correct trials (1.1 ± 0.2) and on error trials (1.2 ± 0.2 , $P = 0.56$). This indicates that, due to later improvement at the chosen target locations on error trials, the attentional competition between chosen and nonchosen locations was resolved later on error trials. Figure 6*B* shows the visual sensitivity difference between chosen and nonchosen locations on correct and on error trials. Clearly, attentional competition between the chosen and nonchosen target was resolved much later on error trials than on correct trials.

To determine whether saccade decisions were biased by selection history, we measured whether target choice was influenced by choice on the previous trial (Fig. 6*C*). For this purpose, we calculated the selection bias as the difference between the percentages of same and different target color or location choices with respect to the previous trial [e.g., a selection bias of 10% would result if a participant selected the same target color on 55% of all trials (instead of 50% expected) and a different target color on 45% of all trials (instead of 50% expected)]. We observed that free choices tended to be biased by the color of the previously chosen target, because participants were less likely to choose the target of the same color (bias: $-3.8 \pm 1.2\%$, $P = 0.002$). Color did not affect rule-based choices on either correct (bias: $0.4 \pm 0.4\%$, $P = 0.26$) or error trials (bias: $1.4 \pm 1.8\%$, $P = 0.42$). The location of the previously chosen target also affected saccade choices, because participants were more likely to choose the same location as on

the previous trial. This was true for free-choice trials (bias: $4.3 \pm 1.0\%$, $P = 0.001$) and for error trials of the rule-based condition (bias: $2.9 \pm 1.5\%$, $P = 0.04$), but not for correct rule-based trials (bias: $0.4 \pm 0.4\%$, $P = 0.32$). Taking these findings together, we observed some small but detectable biases by choice history. Finally, we also measured whether probe presentation on the preceding trial (at a memorized location) could bias saccadic responses on the current trial (errors toward nonmemorized, irrelevant locations). We observed a negligible number of such errors (6 ± 2 trials per participant), which indicates that choice on the preceding trial affected choice on the current trial only if some attributes of the task were shared (target color or target location).

We also calculated whether participants were more likely to choose a saccade target when it coincided with the location of the discrimination probe (Fig. 5*D*). Earlier work has shown that probe presentation typically does not affect the saccadic task (Jonikaitis et al. 2013; Jonikaitis and Theeuwes 2013; Klapetek et al. 2016; Rolfs et al. 2011). We calculated the selection bias as the difference between the percentage of trials in which the selected target coincided with the probed location and the percentage of trials in which the nonprobed location was selected. We observed that on trials where the probe was presented at the location of one of the two targets 50 ms or earlier before the saccade cue (during the memory delay), saccades were more likely to be directed toward the probed target than toward the nonprobed target. This bias was present in the free-choice condition ($17 \pm 5\%$, $P < 0.001$), as well as on correct trials of the rule-based condition ($8 \pm 2\%$, $P < 0.001$), and was strongest on error trials of the rule-based condition ($32 \pm 9\%$, $P < 0.001$). In line with the observation that participants were more likely to choose the probed location as the saccade target, visual sensitivity during the memory delay was higher at the chosen target than at the nonchosen

target (Fig. 6A). This suggests that the good discrimination performance at the upcoming saccade goal during the memory delay was, at least in part, a consequence of the bias to make saccades toward probed locations.

The influence of the probe on decision making was greatly reduced when the probe was presented 50 ms or later after the onset of the saccade cue. In this case, the bias was not significant both on correct trials ($0.3 \pm 0.1\%$, $P = 0.78$) and on error trials of the rule-based condition ($5 \pm 4\%$, $P = 0.12$), and it was even reversed in the free-choice condition ($-6 \pm 3\%$, $P = 0.05$). This can be expected, because it is progressively more difficult to capture attention as more information in favor of the saccade goal has been accumulated (Hunt et al. 2007).

DISCUSSION

The present study investigated the allocation of visuospatial attention during free or rule-based choices between memorized saccade targets. Decision making has been extensively studied in the presence of visual information, that is, when one of two responses has to be chosen while the strength of visual information in favor of both response alternatives is being evaluated (Glimcher 2003; Gold and Shadlen 2007; Schall 2003), but to our knowledge this is one of the few examinations of motor decision making between two goals stored in working memory. In our experiment, no external visual information was available to guide the decision, but we still observed a parallel attentional selection of the competing saccade goals, both before and after the saccade cue. To our surprise, we did not find any substantial differences between the rule-based and free-choice conditions, except for a shorter saccadic latency under free-choice conditions.

Preselection During the Memory Delay

The parallel selection of both saccade targets during the memory delay is consistent with evidence from other studies that spatial attention is allocated to locations maintained in working memory (Awh et al. 1998; Awh and Jonides 2001; Herwig et al. 2010). The design of our experiment does not allow us to disentangle the effects of attention and working memory on discrimination performance, because this was not one of our goals. Moreover, attention and visual working memory show so much overlap at the neural level that many authors consider them to be a unitary or coupled mechanism (Chun 2011; Gazzaley and Nobre 2012; Kiyonaga and Egner 2013; Rensink 2002; Theeuwes et al. 2009; Wheeler and Treisman 2002).

Interestingly, we did not observe a balanced selection of both targets during the memory delay, but one that was biased by future saccadic choice. This shows that on some trials, one target was clearly preferred over the other and that this target was more likely to become the future saccade goal. Target selection was significantly biased by the appearance of the visual probe at one of the two remembered locations and, to a lesser degree, by the color of the saccade goal on the previous trial.

The finding that choice on the previous trial can bias motor decisions has been reported by a number of authors (de Lange et al. 2013; Gallivan et al. 2015; Klaes et al. 2011; Suriya-Arunroj and Gail 2015), and it has been explained by the tendency of subjects to form probabilistic expectations that

shift the starting point of the evidence accumulation closer to the decision boundary (de Lange et al. 2013; Suriya-Arunroj and Gail 2015). Neurophysiological studies have shown that nonsensory variables, such as the prior probability that a certain response will be required (Basso and Wurtz 1998; Dorris and Munoz 1998; Platt and Glimcher 1999), the reward associated with different response alternatives (Platt and Glimcher 1999), or learned space-reward associations (Chelazzi et al. 2014), directly modulate the accumulation of saccade-related evidence in SC and LIP. The traditional dichotomy between top-down and bottom-up influences is not sufficient to explain how attention is allocated and that selection and reward history have to be considered as equally important attentional biases (Awh et al. 2012). Our findings support this notion, because we observed that saccade goal selection was biased by choice on the previous trial, although this bias reduced performance.

We observed that saccadic decisions in our study were not affected by probe presentation during the selection of the saccade target. This finding is consistent with our earlier work, in which we did not observe any effects of discrimination probe appearance on saccade target selection (Jonikaitis et al. 2013; Jonikaitis and Theeuwes 2013; Klapetek et al. 2016; Rolfs et al. 2011). In those earlier studies, the probe did not capture attention, because neither the location of the probe (saccade goal vs. other locations) nor its timing (probes were typically shown at different times during saccade preparation) affected the direction or latency of saccades. In this article we report that the probe did not capture saccades when it was presented during saccade target selection. This indicates that our visual sensitivity measures during this period reflect the allocation of spatial attention.

Furthermore, we observed that saccadic decisions were affected by probe presentation during the memory delay. Participants were more likely to select a target that coincided with the probed location during the memory delay. This effect was quite strong: on free-choice trials, participants were 17% more likely to select a memorized target if the probe had appeared at this target, and in the rule-based condition, such trials accounted for 32% of all errors. The effect occurred only if the probe was presented at an already attended (or memorized) location; probe presentation at other, task-irrelevant locations did not lead to erroneous saccadic decisions. This finding is probably related to contingent attentional capture, a mechanism by which task-irrelevant stimuli can capture attention if they share a contingency with the attentional task (Anderson and Folk 2010; Eimer and Kiss 2008; Folk et al. 1992). Whereas contingent capture has been observed for feature contingencies, such as color or shape, the contingency in our task was spatial location: a location was maintained in memory, and the presentation of a probe at that location subsequently biased the saccadic decision.

Perceptual Selection Reflects the Decision Process

During the decision period, we observed an increase in visual sensitivity at the chosen saccade goal (Castet et al. 2006; Deubel 2008; Deubel and Schneider 1996; Doré-Mazars et al. 2004; Jonikaitis and Deubel 2011; Montagnini and Castet 2007). The time course of this presaccadic visual sensitivity increase was linked to saccade onset regardless of the saccade

latency, which indicates that it reflected the accumulation of sensory information in favor of the saccade goal and/or the saccade program. Surprisingly, we also observed a saccade-related increase in visual sensitivity at the nonchosen target, in both the free and rule-based choice tasks. The increase in visual sensitivity at both the chosen and the nonchosen targets indicates that both locations were evaluated in the oculomotor system as potential saccade targets, even though the decision could have been simply made by retrieving a stimulus-response association stored in memory (e.g., green fixation – look at the previously green location). This suggests that, rather than representing the chosen saccade goal, the oculomotor system represents the decision making process.

Our findings are compatible with previous neurophysiological results showing that visuomotor brain areas simultaneously represent competing or sequential saccade goals (Basso and Wurtz 1998; Kim and Basso 2008; McPeck and Keller 2002; Platt and Glimcher 1997; Sugrue et al. 2004) or reach goals (Baldauf et al. 2008; Cisek and Kalaska 2005; Gallivan et al. 2015; Klaes et al., 2011; Scherberger and Andersen, 2007). Convergent evidence also comes from behavioral research, where parallel saccade programming has been observed in a number of contexts (Becker and Jürgens 1979; Godijn and Theeuwes 2003; Hodgson et al. 2009; Irwin et al. 2000; Massen 2004; McPeck et al. 2000; Morrison 1984; Theeuwes et al. 1998, 1999; Walker and McSorley 2006). We recently reported that parallel saccade programming in the antisaccade task was accompanied by the simultaneous attentional selection of both saccade goals and that the distribution of attention predicted erroneous prosaccades (Klapetek et al. 2016).

An equivalent association between perception and saccade direction was evident in the present study, because both correct and erroneous saccades were preceded by a discrimination benefit at the saccade goal. The fact that vision and saccades tend to select the same spatial locations suggests that they rely on shared decisional mechanisms.

Errors Follow Late Decisions

The general pattern of attentional selection, by which attention was allocated in parallel to both saccade targets, although with a clear benefit at the chosen target, did not differ between trials with correct and erroneous saccades. Nevertheless, visual sensitivity began to rise significantly earlier on correct trials, where it also reached a plateau shortly before the onset of the saccade. Sensitivity on error trials continued to rise until the moment of saccade initiation, which suggests that the competition was resolved at a very late point. Our results suggest that more than 30% of errors in the rule-based condition resulted from a preselection during the delay period that was incongruent with the rule-defined target (see Fig. 5C). The increased competition should take additional time to be resolved. However, the fact that saccadic latencies were shorter on error trials suggests that errors may partly be a consequence of participants prioritizing speed over accuracy, which could have modulated the accumulation rate of the evidence in favor of the erroneous target (Cisek et al. 2009; Hanks et al. 2014; Heitz and Schall 2012). A faster accumulation of evidence for a target on the collicular motor map could be associated with less suppression of other locations via local inhibitory interactions (Sumner 2011), which could explain why erroneous saccades

tended to show less deviation away from the nonselected target than correct saccades (Van der Stigchel et al. 2006).

Attention, Decision Making, or Saccade Programming?

Although it is tempting to ask whether the visual sensitivity modulation during decision making reflects attention, the emerging saccadic decision, or saccade programming, earlier work has shown that these processes are closely associated. The mechanism behind the spatially selective visual sensitivity benefits that we measured has been traditionally considered as visuospatial attention. Current theories of attention are closely linked to the concept of priority maps (Fecteau and Munoz 2006; Serences and Yantis 2006), assuming that certain topographically organized brain areas integrate bottom-up and top-down signals into one or several online representations of the behavioral relevance or priority of spatial locations. In contrast to this type of theories, many decision-theoretic models of visual or saccadic choice posit that the same brain areas transform sensory evidence into saccade programs that compete against each other online. This assumption probably goes too far, because not every decision is automatically transformed into a saccade program (Gold and Shadlen 2003), but it is in principle compatible with the priority map theory: both frameworks describe the situation where multiple stimuli or spatial locations compete for further processing, and both assume that the outcome of the competition is used to guide saccades. Their main difference lies in the degree of their focus on motor actions and in the terminology used to describe the competing neural representations: whereas the former speak of attentional or priority signals, the latter call them decision variables or saccade programs (not claiming that these signals directly drive eye movements). In agreement with this, attention has even been conceptualized as an outcome or byproduct of decisional processes (Fernandez-Duque and Johnson 2002; Krauzlis et al. 2014).

The oculomotor system consists of a network of interconnected cortical and subcortical structures, most of which are known to participate in both visual and oculomotor selection. Neural correlates of decisions have been observed in all parts of the network, including the frontal eye field (Kim and Shadlen 1999; Schall 2003), the supplementary eye field (Coe et al. 2002), area LIP (Platt and Glimcher 1999; Shadlen and Newsome 2001), the superior colliculus (Horwitz and Newsome 1999; Kim and Basso 2008), the prefrontal cortex (Hasegawa et al. 1998; Watanabe and Funahashi 2007), and the caudate nucleus (Ding and Gold 2010; Isoda and Hikosaka 2008). Most of these areas also have been proposed to accommodate a priority map. The final decision where a saccade will be executed is probably accomplished through a distributed consensus between the above-mentioned brain areas, possibly involving a progressive amplification of the difference between target and nontarget representations from the parietal to the frontal cortex and onto the superior colliculus. This process involves a top-down modulation of neural activity in lower visual areas by higher visual areas as well as local neuronal interactions, which have important perceptual consequences and are typically summarized under the term attention (Awh et al. 2006; Carrasco 2011).

In our view, this shows that attention, saccade programming, and saccadic decision making are closely associated and that it

may often be difficult to distinguish between them. We mainly consider it important that theories move away from the traditional view that attention or motor programming are guided by a winner-take-all mechanism, because this view is incompatible with existing results on parallel movement planning and simultaneous attention allocation to multiple locations. Although a winner-take-all mechanism must be necessarily applied during the final selection of the upcoming saccade in motor neurons of the superior colliculus, covert processes, such as visual attention or saccade programming, seem to be guided by the momentary priority of the competing targets or response alternatives.

Conclusions

In the present study, we investigated the allocation of visuospatial attention during decisions between two memorized saccade targets. Attention, as measured by visual sensitivity, was allocated in parallel to the two competing saccade targets, both during the memory delay and in the presaccadic decision period, when the saccade was being programmed.

The distribution of attentional resources was influenced by task requirements, probe appearance, and selection history and predicted the direction of future saccades. During saccade programming, discrimination performance increased gradually at the two potential saccade goals, consistent with a race of both saccade programs toward a decision threshold. Our results therefore indicate that saccade decisions take the form of a biased competition between potential saccade goals, which can begin by a preselection before the saccade cue.

What remains unclear is whether both motor programs are really accumulated in parallel until the last stage of oculomotor programming or whether the second motor program becomes suppressed at some earlier stage. The former strategy would increase the flexibility of saccade planning, for example, when participants would want to change their decision or if they decided to carry out both alternative eye movements in sequence, whereas the latter could speed decisions and prevent errors. Although our results seem to show that both locations competed until the beginning of the saccade, we cannot definitely rule out the possibility that one motor program was suppressed at some intermediate stage of oculomotor programming, because the suppression may not have affected visual perception any more.

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DISCLOSURES

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

AUTHOR CONTRIBUTIONS

D.J. and A.K. performed experiments; D.J. analyzed data; D.J., A.K., and H.D. interpreted results of experiments; D.J. prepared figures; D.J., A.K., and H.D. drafted manuscript; D.J., A.K., and H.D. edited and revised manuscript; D.J., A.K., and H.D. approved final version of manuscript.

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