Title: Evidence for a Link between the Experiential Allocation of Saccade Preparation and Visuospatial Attention

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ABSTRACT

Whether a link exists between the two orienting processes of saccade preparation and visuospatial attention has typically been studied by using either sensory cues or predetermined rules that instruct subjects where to allocate these limited resources. In the real world, explicit instructions are not always available and presumably expectations shaped by previous experience plays an important role in the allocation of these processes. Here we examine whether manipulating two experiential factors that clearly influence saccade preparation – the probability and timing of saccadic responses – also influences the allocation of visuospatial attention. Occasionally, a visual probe was presented whose spatial location and time of presentation varied relative to that of the saccade target. The proportion of erroneous saccades directed towards this probe indexed saccade preparation and the proportion of correct discriminations of probe orientation indexed visuospatial attention. Overall, preparation and attention were significantly correlated to each other across these manipulations of saccade probability and timing. Saccade probability influenced both preparation and attention processes whereas saccade timing influenced only preparation processes. Unexpectedly, discrimination ability was not improved on those trials in which the probe triggered an erroneous saccade despite particularly heightened levels of saccade preparation. To account for our results, we propose a conceptual dual-purpose threshold model based on neurophysiological considerations that link the processes of saccade preparation and visuospatial attention. The threshold acts both as the minimum activity level required for eliciting saccades and a maximum level for which neural activity can provide attentional benefits.

Keywords: oculomotor capture, response probability, visual discrimination, visuospatial attention
Two cognitive processes are important for extracting relevant information from a visual scene: those leading to the overt alignment of the high acuity foveae, accomplished primarily with saccadic eye movements, and those involved in allocating covert shifts of visuospatial attention. How these overt and covert orienting processes are controlled and coordinated at the neural level has long been debated (Klein 1980; Posner 1980). Psychophysical, neurophysiological and neuroimaging studies have conflictingly supported that visuospatial attention and saccade preparation are controlled by neural circuits that are either largely overlapping (Armstrong and Moore 2007; Bisley 2011; Corbetta et al. 1998; Godijn and Theeuwes 2003; Hoffman and Subramaniam 1995; Ignashchenkova et al. 2004; Nobre et al. 2000; Shepherd et al. 1986; Van der Stigchel and Theeuwes 2007) or largely independent of each other (Hunt and Kingstone 2003; Juan et al. 2004; Juan et al. 2008; Klein 1980).

These differing interpretations may arise, in part, from differences in the methodology by which previous experiments have allocated attentional and saccade preparatory processes. Mounting evidence suggests that saccade preparation and visuospatial attention are differently allocated when exogenous cues, such as a flashed peripheral stimulus, rather than endogenous instructions, such as a centrally located arrow or predetermined commands, are used (attention: Funes et al. 2007; Hunt et al. 2007; Hunt et al. 2003; Taylor and Klein 2000; saccade preparation: Barton et al. 2006; Munoz and Everling 2004; Theeuwes et al. 1998; Shepherd et al. 1986). For example, exogenous cues reflexively attract attention, followed by an extended period in which
attention is “inhibited” from the cued location. This phenomenon of ‘inhibition of return’ is not observed during endogenous cueing (Taylor and Klein 2000).

The present experiment examines how saccade preparation and attention processes are allocated by expectations that arise from previous situational experience rather than explicit instructions. To accomplish this, we introduced two regularities in the experimental environment upon which subjects could form expectations to guide these orienting processes. First, saccade timing was predictable because of a fixed 600 ms warning period that preceded target presentation. Second, saccade probability was manipulated by varying the likelihood of targets being presented at particular locations across blocks of trials. Indeed, previous studies have shown that saccade preparation processes are lawfully influenced by both saccade timing (Janssen and Shadlen 2005; Roesch and Olson 2005; Thevarajah et al. 2009) and probability (Basso and Wurtz 1998; Carpenter and Williams 1995; Dorris and Munoz 1998). The issue that we address here is whether the allocation of visuospatial attention is coupled to that of saccade preparation when the regularities introduced into the task are only predictive of saccade targets.

METHODS

Sixteen human subjects with self-reported normal or corrected to normal vision participated in this experiment (10 female, 6 male, ages 20-35, including the three authors). During each 45-minute session, subjects completed 3 blocks of 220 experimental trials. In total, they performed 6 training blocks to become familiar with the experimental procedure, followed by the 15 experimental blocks reported here. The
subjects received $3 per block, amounting to $63 of total payment per subject. The
Queen’s University Human Research Ethics Board approved all experimental procedures
and informed consent was obtained from all subjects.

General Methods

Subjects faced a computer monitor (refresh rate of 100Hz) while seated in a
comfortable chair with their head stabilized on a chin rest. The monitor was positioned 59
cm in front of the subjects and spanned 32° of their visual field. We monitored left eye
position using an Eyelink II infrared eye tracker (SR Research) with a 250 Hz temporal
resolution and a 0.025° RMS spatial resolution. A Pentium 4 computer running real-time
data acquisition software (Gramalkn, Ryklin Software) controlled all behavioral
paradigms, visual displays and data storage. Data analysis was conducted with Matlab
version R2006a (Mathworks Inc.), and statistical analysis conducted with SigmaStat
version 3.11 (Systat Software Inc.).

Behavioral Paradigms

Subjects were required to saccade to a target whose probability of being presented
to the left or right, defined as saccade probability, varied across blocks of trials.
Importantly, subjects were not informed that saccade probability varied across blocks nor
were they given instructions on how to allocate saccade preparation and attentional
resources. To probe the allocation of visuospatial attention, subjects were also required to
discriminate, with a button press, the orientation of a peripheral visual probe that was
occasionally presented. Each block consisted of randomly interleaved control trials (70% - Fig. 1A) and probe trials (30% - Fig. 1B), the details of which are outlined below.

Control Trials

During control trials, subjects initially fixated a central fixation point (0.5° visual diameter, 5.2 cd/m² luminance, Red:225, Green:0, Blue:0) for 800ms. The fixation point was then extinguished and 600 ms later a saccadic target with identical attributes as the fixation point was presented 8° to either the left or right of center. This 600ms warning period facilitated saccade preparation both by acting as a general warning signal and by releasing active fixation (Dorris et al. 1997; Saslow 1967). The probability of the target appearing left/right of center was manipulated between blocks of trials (100%/0%, 80%/20%, 50%/50%, 20%/80% 0%/100%) but, within each block, saccade probability remained constant. Blocks were pseudo-randomly interleaved so that each subject completed 3 blocks of each probability combination. Finally, there was a 1000ms inter-trial interval. If subjects failed to maintain gaze position on the fixation point or throughout the warning period (±3°), the trial was immediately aborted.

Probe Trials

Probe trials served the dual purpose of providing indices of both saccade preparation and visuospatial attention, as outlined below. Probe trials were identical to control trials with two exceptions. First, a visual probe was briefly flashed during the warning period and the subject was required to perform a visual discrimination on the orientation of this probe at the end of the trial. Second, the target stimulus reappeared at
the fixation location at the end of the warning period instead of peripherally. This both reminded the subject that they should not direct a saccade to the probe and controlled for any differences in discrimination ability that could be associated with peripheral targets and probes that were either in or out of spatial register. The probe took the form of a green, Landolt open-ring optotype (0.5° visual diameter, 5.2 cd/m² luminance, R:0, G:225, B:0) whose gap was equally likely to be facing up or down. The probe was presented for 70ms, an interval too short in which to acquire it with a saccade. In addition, it was immediately followed by a pixilated visual mask for 70ms which prevented retinal afterimages from aiding visual discrimination of the probe. During the training sessions, gap size was adjusted for each individual subject until they could correctly discriminate on 60-70% of trials across all three probe positions and this gap size was then fixed for the remainder of the experimental sessions. Probe location was equally likely to be at the location of potential saccadic targets (8° left (33⅓ %) or right (33⅓ %) of center) or at an orthogonal location where saccadic targets were never presented (8° up (33⅓ %) of center). Moreover, probe timing was equally likely to be presented early (200ms), middle (400ms), or late (600ms) into the 600ms warning period. Note that when the probe was presented late in the warning period, reappearance of the target at the fixation location was delayed by 140ms so its abrupt onset did not interfere with probe discrimination.

Data Analysis

The first 20 trials of each block were excluded from analysis, allowing subjects time to adapt to the new target probabilities. Data were collapsed across the left/right
direction. For example, leftward data from a block of 80% left saccade probability were combined with rightward data from a block of 20% left saccade probability.

*Saccade initiation* was defined as the time at which eye velocity first surpassed 30º/s. *Correct saccades* were defined as the first saccade between 70ms and 300ms after target onset that ended within 3º of the target. Saccades initiated before 70ms were considered anticipatory and the trial was immediately aborted and not considered in subsequent analyses. Less than 2% of trials fell in this category. *Saccadic reaction times (SRTs)* were defined as the time between the presentation of a peripheral stimulus and the initiation of a stimulus directed saccade. This stimulus was the target for controls trials and the probe for probe trials. *Manual reaction times (MRTs)* were defined as the time between probe presentation and the registering of a valid button press. Although subjects were instructed not to look towards the visual probes, occasionally they did so. *Oculomotor captures* were defined as saccades that were directed towards the probe and that were initiated within 300ms of its appearance. Spatial constraints were relaxed (i.e., from ±3º to ±5º) for oculomotor captures because these saccades tend to be hypometric relative to target-directed saccades (Theeuwes et al. 1998; Milstein and Dorris 2007).

Quantifying Saccade Preparation and Visuospatial Attention

Saccade preparation was quantified using two different measures: target-directed SRTs during control trials and the proportion of oculomotor captures during probe trials. The proportion of oculomotor captures is thought to reflect the underlying level of saccade preparation at the time and location of probe presentation (Dorris et al. 2007; Milstein and Dorris 2007). Similarly, the proportion of correct probe
discriminations is thought to reflect the level of visuospatial attention allocated at the time and location of probe presentation (Ignashchenkova et al. 2004; Yeshurun and Carrasco 1999).

RESULTS

The results are organized into three sections. The first section investigates how saccade probability influences the allocation of saccade preparation using two behavioral indices. SRTs measure the level of saccade preparation at the location and time of target presentation. Oculomotor captures provide additional information of how saccade preparation evolves temporally as the time of target presentation approaches and at locations other than where the targets were presented. In the second section, visuospatial attention was quantified in a similar manner using the accuracy of probe discriminations. In the third section, any relationship between saccade preparation and visuospatial attention processes will be investigated by correlating oculomotor captures with probe discriminations.

The Influence of Temporal and Spatial Expectations on Saccade Preparation

Three aspects of the task facilitated the advanced allocation of saccade preparation. First, the majority of trials required saccade generation (70% control trials) whereas only the minority required attentional discrimination (30% probe trials). Second, the warning period predicted when the saccade target would be presented but not probe timing. Finally, saccade probability was predictive of upcoming saccade direction whereas probes were always equally likely to be presented at three spatial locations.
The influence of saccade probability on the allocation of saccade preparation was first indexed by target-directed SRTs during control trials. As can be seen qualitatively from the eye traces of a representative subject, SRTs were shorter towards targets of high probability than towards targets of low probability (Fig 2A). Less than 3% of saccades were in the express saccade range of 70-120ms (Fischer and Ramsperger 1984) across all probabilities (Table 1). We normalized SRTs to the 100% condition for each subject to examine the effects of probability on SRTs across subjects (Fig. 3). There was a significant effect of probability on SRT [Fig 3, One-way RM ANOVA, $F(4,11)=13.5$, $p<0.001$]. In addition, 13 of the 16 individual subjects showed a significant change in SRT with saccade probability ($p<0.01$).

The second measure of saccade preparation was the proportion of oculomotor captures triggered during probe trials. This index of saccade preparation was more relevant for our purposes because it was during these same probe trials that visuospatial attention was assessed. Similar to target-directed SRTs, probes presented at locations of higher saccade probability induced more oculomotor captures than probes presented at locations of lower saccade probability (Fig 2B). Consistent with previous literature (Milstein and Dorris 2007; Theeuwes et al. 1998), oculomotor captures had shorter SRTs (ANOVA, $p<0.01$) and a higher percentage of express saccades ($p<0.01$) than probability-matched target-directed saccades (Table 1). Overall, there was no relationship between saccade probability and SRTs of ensuing oculomotor captures ($r = -0.056$, $p = 0.07$). Because the goal of this study is to investigate whether saccade preparation influences visuospatial attention, only those 12 subjects whose proportion of oculomotor
captures were significantly affected by saccade probability were included in the remainder of the analyses ($\chi^2$ test, $p<0.05$).

We examined how oculomotor captures were influenced by both saccade probability and probe timing during the warning period. First, oculomotor captures were more likely to be directed towards probes presented at potential target locations (Fig 4A – black line) than non-target locations [Fig 4B – black line, $t(8) = -8.3, p<0.001$]. Second, there was a significant main effect of probability [Two-way RM ANOVA $F(4,11)=52.4, p<0.001$], and probe timing [$F(2,11)=85.0, p<0.001$] on oculomotor captures directed towards left/right probes that did not exist for the up probes [Two-way RM ANOVA probability: $F(4,11)=0.6, p=0.6$; probe timing: $F(2,11)=2.3, p=0.124$] Third, an interaction between probability and probe timing was also present only for oculomotor captures towards left/right probes [$F(8,11)=4.7, p<0.001$]. Lastly, probes presented later in the warning period evoked shorter SRTs when oculomotor captures are triggered ($r = -0.33, p < 0.001$) although probe SRTs were not affected by saccade probability (see above). Together, these results demonstrate that saccade preparation was allocated preferentially towards potential targets, was influenced by saccade probability, and accumulated as the time of target presentation approached.

The Influence of Temporal and Spatial Expectations on Visuospatial Attention

In the previous section, we observed an effect of both saccade probability and probe timing on the proportion of oculomotor captures. Analyzing the same probe trials, we now examine whether the ability to successfully discriminate follows the same probabilistic and time courses as saccade preparation.
Discrimination ability was significantly improved when probes were presented at potential target locations than at non-target locations [Fig 5A – black line vs. Fig 5B – black line, t(8) = -7.2, p<0.001]. Subjects performed above chance level in all probability and timing conditions when probes were presented at potential target locations ($\chi^2$ test, $p < 0.05$), whereas the same was true for only two of the fifteen conditions when probes were presented in non-target locations (Fig 6). Probes presented at potential target locations were significantly affected by probability [Two-way RM ANOVA, $F(4,11)=4.0$, $p=0.007$] but not probe timing [$F(2,11)=1.2, p=0.321$] and no interaction existed between the two [$F(8,11)=0.4, p=0.892$]. On the other hand, there was no main effect of probability [Two-way RM ANOVA $F(4,11)=1.5, p=0.233$] or timing [Two-way RM ANOVA $F(2,11)=0.3, p=0.742$] on the ability to discriminate probes presented at the non-target location (Fig 5B). We also did pairwise Bonferroni-corrected t-tests (where significance was set at $p<0.05/3$ or 0.017) comparing all timing conditions. We found no significant effects although there was a trend between the 200 and 600 ms probe times for the 20% ($p=0.04$) and 50% ($p=0.13$) conditions. Together, these results demonstrate that, like saccade preparation, visuospatial attention was preferentially allocated toward potential targets and was influenced by saccade probability. However, visuospatial attention was not influenced by task timing as was observed for saccade preparation.

**Correlation between Saccade Preparation and Visuospatial Attention**

A correlation between oculomotor captures and probe discriminations would provide evidence for a link between saccade preparation and visuospatial attention. Indeed, a statistically significant correlation existed between these two measures for
probes presented at potential target locations (Fig 6, solid symbols, $r=0.66, p<0.01$) that
was absent for probes presented at the non-target upward location (Fig 6, hollow symbols,
$r=0.14, p=0.62$). This analysis suggests that, irrespective of saccade probability or timing,
overall changes in one cognitive process are reflected in the other.

To further test the relationship between saccade preparation and visuospatial
attention, we examined the ability to discriminate on trials in which an oculomotor
capture was triggered by the probe compared to those in which a saccade was
successfully withheld. Previous behavioral (Milstein and Dorris 2007) and
neurophysiological (Dorris et al. 2007) studies suggest that saccade preparation is
increased preceding oculomotor captures. If saccade preparation and visuospatial
attention share underlying neural circuitry then probe discrimination should be improved
for trials in which the probe triggered an oculomotor capture than those in which it did
not.

To provide sufficient statistical power, analysis was limited to blocks in which
there were at least 10 trials in which the probe triggered oculomotor captures and 10 in
which it did not. A total of 64 blocks met this criterion. The proportion of correct
discriminations following oculomotor captures was compared with the proportion of
correct discriminations when fixation was maintained. In just over half of these blocks
(33/64 blocks), discrimination was better following oculomotor captures but this
improvement did not reach statistical significance ($z = 1.8, p = 0.86$). This finding was
unchanged when we repeated this analysis with reduced (e.g., 5 trials) or increased (e.g.,
15 trials) number of trials in each category.

Lastly, we sought evidence of modulated attention in our task in manual reaction
times. Decreased manual reaction times have been a hallmark of increased spatial attention in a number of studies (see Posner 1980). During correct discrimination trials, we expected shorter manual reaction times would accompany oculomotor capture trials when attentional allocation was presumably higher. However, we found that manual reaction times were significantly higher when an oculomotor capture was triggered than not ($t = 9.50, p < 0.001$). This unexpected result may reflect an interference of the oculomotor capture itself on manual reaction time.

Similarly unexpected, there was no difference in oculomotor capture saccade reaction times between correct and incorrect discrimination trials ($p = 0.098, t = 1.66$). Therefore, there does not appear to be enhanced attention as measured with either saccadic or manual responses in our task when a probe triggers or does not trigger an oculomotor capture.

**DISCUSSION**

Overall, our results demonstrate that visuospatial attention is linked to the experiential allocation of saccade preparation, thus supporting the viewpoint that these two processes share overlapping neural circuits. We use the term experiential because saccade preparation was allocated based on prior probability and expected timing rather than by immediate sensory cues or explicit instructions as is typical of many other studies. The probability and timing of saccade targets influenced saccade preparation as evidenced by the patterns of SRTs (Fig 3) and oculomotor captures (Fig 4A). Similarly, the probability of saccade targets also influenced visuospatial attention as evidenced by the subject’s ability to discriminate probes, although probe timing did not significantly
influence discrimination ability (Fig 5A). Most tellingly, there was a correlation between the indices of saccade preparation and visuospatial attention irrespective of saccade probability and probe timing (Fig 6). These findings are important because they demonstrate that both saccade preparation and visuospatial attention can be co-allocated based on situational experience, which is presumably an important, if not the primary, means by which these orienting processes are directed outside the laboratory (Hasson et al. 2008; Underwood et al. 2003).

Below, we outline a conceptual model based on physiological considerations that captures many of these diverse experimental findings. In this model, both saccade preparation and visuospatial attention processes are subserved by the same neural activations. Its defining feature is that a single threshold level serves the dual purposes of demarcating the floor for triggering saccades and the ceiling for attentional benefits. This attentional ceiling, in particular, helps explain why little improvement in discrimination ability was observed on trials in which oculomotor captures occurred despite presumably heightened saccade preparatory activity.

**Dual-Purpose Threshold Model Linking Saccade Preparation and Visuospatial Attention**

Our proposed model is based on the firing rates across time of neural structures whose activities represent a topographically organized map of saccade generation and also respond to the presentation of visual stimuli. Several neural structures within the visuosaccadic system are organized as topographic maps (Colby and Goldberg 1999; Glimcher 2003; Schall and Thompson 1999). This visuosaccadic network is highly...
distributed and interconnected so we would not expect one structure to be solely responsible for all our observed effects. That being said, we chose the intermediate layers of the superior colliculus (SCi), a neural structure at the motor end of the visuosaccadic continuum, to illustrate the physiological properties of our model. We chose this relatively motor structure because the primary action associated with our task was saccade generation, however, the SCi is also involved in attentional processing (e.g., Ignashchenkova et al. 2004; Kustov and Robinson 1996) that would be required for visual discrimination of the occasional probe. Brain areas with weaker visual bursts and further from the saccadic threshold (e.g. area LIP) would not be as suitable for our purposes.

Our model is outlined schematically in Figure 7. The hypothetical activity of a group of neurons representing one of the target locations during control trials is shown for the 5 probability conditions in Figure 7A. We assume that reciprocal activity patterns occur for the group of neurons associated with the probability of the opposite target appearing. Figure 7B shows activity of the same group of neurons during probe trials when probes are presented in the neurons’ response field. This schematic has five important characteristics.

First, activation increases steadily throughout the warning period beginning approximately 100ms after fixation point offset and as the known timing of target presentation approached (Fig 7A; Dorris and Munoz 1998). Such low frequency SCi activity correlates with saccade preparation (Dorris et al. 1997; Dorris and Munoz 1998) and visuospatial attention (Ignashchenkova et al. 2004; Kustov and Robinson 1996).

Second, the rate at which this advanced activity accumulates scales with saccade
probability (Fig 7A; Dorris et al. 1998). Third, shortly after the presentation of the probe (~60ms) a transient burst of activity occurs at the corresponding SCi location (shaded region Fig 7B). This transient burst is additive with the pre-existing advanced activity (Dorris et al. 1997; Dorris et al. 2007). Fourth, neurons exhibit trial-by-trial variability in their firing rate (Shadlen and Newsome 1998). This noise is important because, without it, activity would deterministically either always or never surpass saccadic threshold for a given combination of saccade probability and probe timing. This variance can be approximated by multiplying the mean count by a constant (Shadlen and Newsome 1998).

This is exemplified for our model by the red shaded area in figure 7A.

Finally, and most importantly, we propose that a single threshold both demarcates the floor for triggering saccades and the ceiling for attentional benefits.

Neurophysiological support for a saccade threshold comes from the increased preparatory activity and probe-related transient burst observed when the probe triggers an oculomotor capture than when it does not (Fig 7B; Dorris et al. 2007). The proposal that this same threshold acts as a ceiling for peripheral attention follows from two lines of logic. First, visual perception and accompanying attentional processing is known to be suppressed throughout the duration of saccades (Zuber and Stark 1966). Second, it is unnecessary to analyze targets of interest with peripheral attention once a saccade is initiated because this can be accomplished with foveal processing.

Together, our model proposes that, as the probability of target presentation increases and as the time of target presentation approaches, the baseline activity steadily increases. Elevated baseline activity, in turn, increases the likelihood that the visual transient produced by sudden presentation of a probe surpasses the dual-purpose
threshold and triggers an oculomotor capture. This conceptual framework accounts for
the observed effects of probe timing and saccade probability on oculomotor captures (Fig
4). The rapid onset of the visual transient is such that, if it does surpass threshold, this
occurs so quickly that there is little difference in oculomotor capture reaction times in
terms of probe timing or saccade probability. If, however, the visual transient does not
surpass the dual-purpose threshold, the activity level is positively correlated to attentional
benefits. This is consistent with our main observation that visuospatial attention is
correlated with saccade preparation (Fig 6).

Importantly, attentional benefits saturate with increasing activity. This saturation
in attentional benefits occurs as a consequence of having a threshold that acts as a ceiling
and could explain why discrimination ability did not improve significantly on oculomotor
capture trials than on those without. Upon first inspection, this result appeared to provide
evidence against a link between saccade preparation and visuospatial attention as
elevated saccade preparation on these trials was not accompanied by improved
discrimination ability. However, most blocks of trials that had sufficient numbers of both
oculomotor capture trials and non-oculomotor capture trials to contribute to this analysis
presumably had average activation levels very close to the threshold where attentional
benefits were nearly saturated. A ceiling effect is also supported by the fact that both
saccadic and manual reaction times were not shorter for correct discriminations on those
trials in which an oculomotor capture was triggered.

In a similar manner, this ceiling effect could also explain why attentional benefits
appear to saturate as the time of target presentation approaches. We observed a possible
trend for a timing effect across the 200 and 600 ms times at lower target probabilities that
disappeared at higher target probabilities (i.e., see the compression of data points as saccade probability increases in Fig. 5). At higher target probabilities activity may be already close to the threshold ceiling for attentional benefits. Therefore, any further timing effects will only increase the proportion of oculomotor captures whereas attentional benefits are limited by the threshold.

Conclusions

This study adds to the growing body of knowledge concerning the experiential allocation of both saccade preparation and visuospatial attention. Previous studies have demonstrated that the probability of probe location, rather than saccade target location as used here, influenced the allocation of attention (Ciaramitaro et al. 2001). Our neurophysiology based conceptual model of this link between the two orienting processes is supported by results showing that activity of visuomotor cells in the SC are modulated by attentional cues (Ignashchenkova et al. 2004; Kustov and Robinson 1996) and stimulation of the frontal eye fields, an area generally associated with driving purposive saccades, improves visual discrimination (Moore and Fallah 2004). Our results suggest that saccade preparation and visuospatial attention is tightly linked. Further research is needed to fully characterize any additional differences that may exist in co-allocating saccade preparation and visuospatial attention when guided by experience rather than by instructions.

In conclusion, we found that saccade probability affected both the proportion of oculomotor captures and the ability to visually discriminate therefore providing support for overlapping neural circuits between the allocation of saccade preparation and
visuospatial attention. Their allocation differ in certain respects, however, as the effect of timing differed between the two processes. These findings extend previous work that indicated a link between these two processes, by demonstrating that this relationship holds when these processes are allocated based on previous experience rather than immediate sensory cues or previous instructions. Here, we proposed a conceptual model in which attention and saccade preparation share both a common neural substrate and a dual-purpose threshold to account for how these orienting processes are allocated based on experience.
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**FIGURE LEGEND**

**Figure 1**: Schematic of behavioral paradigm. Each panel denotes a successive display on a computer monitor. The red arrow represents target-directed correct saccades and the green arrow represents probe-directed oculomotor captures. Semi-transparent stimuli were not actually presented on the computer monitor but denote possible locations of targets and probes. (A) Control trials. (B) Probe trials were the same as control trials with the following exceptions. First, a probe in the form of a landolt C was flashed for 70ms followed by a 70ms pixelated mask. Second, the saccade target re-appeared centrally instead of peripherally. Subjects indicated the perceived orientation of the gap in the Landolt C with a keyboard press at the end of the trials.

**Figure 2**: Eye traces from an individual subject across 5 saccade probability blocks. Each block is segregated into (A) control trials and (B) probe trials. Upward traces indicate rightward saccades and downward traces indicate leftward saccades. Green traces indicate probe-directed oculomotor captures and red traces target-directed correct trials. The time of target and probe presentations are denoted by the red and green vertical lines, respectively. The three times of probe presentations are presented in different shades of green and are reflected in oculomotor capture traces. The stippled blocks following probe presentation indicate timing of the mask. The red shaded window represent the time during which saccade initiation must have occurred to be classified as a correct saccade.
**Figure 3**: Influence of saccade probability on SRT. Each subject's data was normalized to their mean SRT at 100% probability, which is denoted by the black dashed line. N=16 subjects.

**Figure 4**: Influence of saccade probability and probe timing on oculomotor capture. The data is segregated based on whether probes were presented at (A) potential target locations and at (B) non-target locations. Black - average of all probes; blue - early (200ms) probes; green - middle (400ms) probes; red - late (600ms) probes.

**Figure 5**: Influence of saccade probability and probe timing on probe discriminations. The data is segregated based on whether probes were presented at (A) potential target locations and at (B) non-target locations. Black - average of all probes; blue - early (200ms) probes; green - middle (400ms) probes; red - late (600ms) probes. Same 12 subjects and probe trials as Figure 4.

**Figure 6**: Relationship between saccade preparation and visuospatial attention indices. Each data point represents a combination of probe timing (blue - early; green - middle; red - late), saccade probability (circle - 100%; triangle - 80%; square - 50%; diamond - 20%; star - 0%), and probe location (filled - left/right; unfilled - up). The least squares regression is fit to the left/right data, and not the up data. The black dotted line denotes chance discrimination.
Figure 7: Dual-purpose threshold model. (A) Schematic of dual-purpose threshold model (see text for details). Activity represents the level of both visuospatial attention and saccade preparation associated with a potential target location. Activity associated with different target probabilities are represented by different colors (red - 100%; navy - 80%; pink - 50%; green - 20%; blue - 0%). The red shaded region indicates one standard error from the mean firing rate at the 100% condition. Increasing intensity of the gray gradient indicates increasing attentional benefits. (B) Activity of the same group of neurons when a probe was presented in the neuron's response field 600ms into the warning period. The shaded area highlights the transient burst following probe presentation. Data was segregated into trials in which subjects successfully remained on fixation (solid line) and trials in which probes elicited an oculomotor capture (dashed line).
Table 1. Average SRT and percent express saccades for correct target-directed saccades and probe-directed oculomotor captures.

<table>
<thead>
<tr>
<th></th>
<th>100%</th>
<th>80%</th>
<th>50%</th>
<th>20%</th>
<th>0%</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Target SRT</strong></td>
<td>190.26 ± 0.47 ms</td>
<td>191.87 ± 0.49 ms</td>
<td>197.39 ± 0.64 ms</td>
<td>201.79 ± 1.11 ms</td>
<td>N/A</td>
</tr>
<tr>
<td><strong>Probe SRT</strong></td>
<td>182.15 ± 3.09 ms</td>
<td>191.41 ± 3.40 ms</td>
<td>185.95 ± 2.47 ms</td>
<td>180.11 ± 3.42 ms</td>
<td>192.46 ± 3.61 ms</td>
</tr>
<tr>
<td>% Express to Target</td>
<td>2.6%</td>
<td>1.1%</td>
<td>0.54%</td>
<td>0.49%</td>
<td>N/A</td>
</tr>
<tr>
<td>% Express to Probe</td>
<td>11.22%</td>
<td>5.21%</td>
<td>6.23%</td>
<td>13.81%</td>
<td>6.56%</td>
</tr>
</tbody>
</table>
Probe-Directed Oculomotor Capture
Maintain Fixation: Correct Trial

Control Trials (70%)

Probe Trials (30%)

Warning Period (600ms)

200, 400 or 600ms

Probe 70ms

Mask 70ms

Probe-Directed Oculomotor Capture

Maintain Fixation: Correct Trial

Spatial Discrimination