1 **LINKING EXPRESS SACCADE OCCURANCE TO STIMULUS PROPERTIES**
2 **AND SENSORIMOTOR INTEGRATION IN THE SUPERIOR COLLICULUS**
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48   **ABSTRACT**

49

50   Express saccades represent the fastest possible eye movements to visual targets

51   with reaction times that approach minimum sensory-motor conduction delays. Previous

52   work in monkeys has identified two specific neural signals in the superior colliculus (SC:

53   a midbrain sensorimotor integration structure involved in gaze control) that are required

54   to execute express saccades: 1) *pre-visual activity* consisting of a low frequency increase

55   in action potentials in sensory-motor neurons immediately prior to the arrival of a visual

56   response; and 2) *a transient visual-sensory response* consisting of a high frequency burst

57   of action potentials in visually responsive neurons resulting from the appearance of a

58   visual target stimulus. In order to better understand how these two neural signals interact

59   to produce express saccades, we manipulated the arrival time and magnitude of visual

60   responses in the SC by altering target luminance and we examined the corresponding

61   influences on SC activity and express saccade generation. We recorded from saccade

62   neurons with visual, motor and pre-visual related activity in the SC of monkeys

63   performing the gap saccade task while target luminance was systematically varied

64   between 0.001 cd/m^2 and 42.5 cd/m^2 against a black background (~0.0001 cd/m^2). Our

65   results demonstrated that: 1) express saccade latencies were linked directly to the arrival

66   time in the SC of visual responses produced by abruptly appearing visual stimuli; 2)

67   express saccades were generated toward both dim and bright targets whenever sufficient

68   pre-visual activity was present; and 3) target luminance altered the likelihood of

69   producing an express saccade. When an express saccade was generated, visuomotor

70   neurons increased their activity immediately prior to the arrival of the visual response in

71   the SC and saccade initiation. Furthermore, the visual and motor responses of visuomotor

72   neurons merged into a single burst of action potentials, while the visual response of

73   visual only neurons was unaffected. A linear combination model was used to test which

74   SC signals best predicted the likelihood of producing an express saccade. In addition to

75   visual response magnitude and pre-visual activity of saccade neurons, the model

76   identified pre-saccadic activity (activity occurring during the 30ms epoch immediately

77   prior to saccade initiation) as a third important signal for predicting express saccades. We

78   conclude that express saccades can be predicted by visual, pre-visual and pre-saccadic

79   signals recorded from visuomotor neurons in the intermediate layers of the SC.

80

81

82   **INTRODUCTION**

83   Express saccades reflect the fastest visually triggered saccadic eye movements in

84   primates with latencies that approach the minimum efferent and afferent conduction

85   delays between the retina and the extra-ocular muscles (Fischer and Boch 1983; Fischer

86   and Weber 1993; Paré and Munoz 1996; Dorris et al. 1997). Here, the neural processing

87   times that would otherwise be necessary to make higher order decisions about the

88   meaning of stimuli or how to respond to them are bypassed. Thus, express saccades

89   represent a "visual grasp reflex" (Hess et al. 1946) whereby abruptly appearing visual

90   stimuli are directly transformed into saccadic motor commands to move the eyes toward

91   them (Edelman and Keller 1996; Dorris et al. 1997; Sparks et al. 2000).

92   The superior colliculus (SC) is an oculomotor control structure in the midbrain

93   that integrates sensory, motor, and cognitive signals related to visual orienting (Hall and

94   Moschovakis 2003; Gandhi and Katnani 2011; White and Munoz 2011; Krauzlis et al.

95   2013). The SC is an ideal candidate for directly translating visual to motor activity during

96   express saccades because it receives early visual input via the retino-tectal and retino-

97   geniculo-cortico-tectal pathways (Fries 1984; Cusick 1988; Robinson and McClurkin

98   1989; Lock et al. 2003) and visuomotor neurons in the intermediate layers (SCi) project

99   directly to the saccadic brainstem burst generator to drive saccades (Rodgers et al. 2006).

100   Furthermore, the SC is critical in the generation of express saccades because when it is

101   lesioned, express saccades are abolished (Schiller et al. 1987).

102   Visual neurons that lack saccade responses are believed to reside in the superficial

103   SC (SCs) and reflect visual signals at an earlier stage of sensorimotor processing relative

104   to visuomotor neurons in the SCi (Boehnke and Munoz 2008). Because these visual only

105   neurons do not exhibit motor activity, a change in their visual response between regular

106   and express saccades would indicate that express saccades are influenced at an early

107   stage of visual processing. Because neural correlates with express saccades have only

108   been reported in neurons with motor related activity in the SCi (Dorris and Munoz 1995;

109   Edelman and Keller 1996; Dorris et al. 1997; Sparks et al. 2000), we hypothesize that

110   express saccades are triggered at a later stage of sensorimotor integration that is closer to

111   the motor output. Consequently, the visual response in visual only SC neurons should be

112   unaffected across regular and express saccades.

113   Historically, express saccades have been defined using behavioral criteria;

114   specifically, the presence of multiple modes within a distribution of saccade latencies

115   (Fischer and Boch 1983; Fischer and Ramsperger 1984). However, more recently it was

116   suggested that this definition is incomplete and that an expanded definition links express

117   saccades to the temporal occurrence of visual responses in the SCi (Edelman and Keller

118   1996; Dorris and Munoz 1998; Sparks et al. 2000). Regular latency saccades have longer

119   latencies than express saccades. During a visually-triggered regular latency saccade, high

120   frequency bursts of action potentials related to visual target appearance and saccade onset

121   can be observed as temporally separate events on SCi visuomotor neurons (Fig. 1; blue

122   traces). However, during an express saccade, these visual and motor responses temporally

123   merge (Edelman and Keller 1996; Dorris et al. 1997; Dorris and Munoz 1998; Sparks et

124   al. 2000), to produce a single burst of action potentials. This merged response is often of

125   higher frequency than the distinct and temporally separate visual and motor responses

126   that are observed during regular latency saccades (Fig. 1; red traces). Because the motor

127   response that drives an express saccade is time locked to the visual response (Edelman

128   and Keller 1996; Dorris and Munoz 1998; Sparks et al. 2000), which correspondingly

129   changes with stimulus luminance (Bell et al. 2006; Li and Basso 2008; Marino et al.

130   2012a; Tanaka et al. 2013), we hypothesize that express saccade latencies are not fixed to

131   a specific temporal range, but are instead dependent on stimulus specific visual response

132   onset latencies in the SCi.

133   Increases in low frequency (<100 Hz) SCi activity prior to the appearance of a

134   visual target also influences express saccade generation (Dorris et al. 1997; Dorris and

135   Munoz 1998). This pre-visual activity (Fig. 1; red traces) increases relative to the amount

136   of predictive foreknowledge of where or when a visual target will appear (Dorris and

137   Munoz 1998; Basso and Wurtz 1998) and has been shown to correlate with increased

138   express saccade likelihood (Dorris et al. 1997). These observations have led to the

139   development of a threshold based model for express saccade generation in the SCi (Fig.

140   1B). In this model, an express saccade is generated when a visual response is

141   significantly large enough to cross a neural trigger threshold and initiate a visually guided

142   saccade (Edelman and Keller 1996; Dorris and Munoz 1998). When added to pre-visual

143   activity, the peak of the visual response is increased, thereby making it even more likely

144   to cross threshold and trigger an express saccade. Without sufficient pre-visual activity,

145   it is less likely that a visual response in isolation would be strong enough to cross this

146   saccade threshold (Dorris et al. 1997; Dorris and Munoz 1998). Based on this hypothesis,

147   both the magnitude of the visual response and the amount of accumulated pre-visual

148   activity should combine to determine whether an express saccade is triggered.

149   Here, we examine this hypothesis by testing how changes to the magnitude and

150   timing of the visual response and the amount of accumulated buildup activity interact to

151 influence express saccade production. This was accomplished by systematically

152 manipulating target luminance in a gap task that facilitates express saccade generation.

153 Because altered target luminance modulates the onset latency of visual responses (Gawne

154 2000; Bell et al. 2006; Lee et al. 2007; Li and Basso 2008; Marino et al. 2012a; Tanaka et

155 al. 2013), the amount of time available for pre-visual activity to accumulate also changes.

156 We hypothesize that express saccades can still be performed toward dim targets because

157 weaker visual responses can be compensated for by increased pre-visual activity that

158 continues to accumulate in the gap task when the visual response is delayed.

159

160 **METHODS**

161 **Animal preparation**

162   All animal care and experimental procedures were in accordance with the

163 Canadian Council on Animal Care policies on use of laboratory animals and approved by

164 Queen's University Animal Care Committee. Three adult male monkeys (Macaca

165 mulatta 5-7 yrs, 8-12 Kg) were trained to perform several oculomotor tasks. Data from 2

166 out of 3 of the monkeys has been published previously (Marino et al. 2012a).The surgical

167 techniques required to prepare animals for neuronal and eye movement recordings in our

168 laboratory have been described previously (Marino et al. 2008). In brief, all animals

169 underwent surgery under aseptic conditions for the insertion of eye coils, a stainless steel

170 head holder, and a recording chamber that was mounted on the skull using stainless steel

171 bone screws and dental acrylic. The recording chamber was oriented towards the SC at an

172 angle of 38° posterior of vertical in the mid-sagittal plane. Monkeys were given at least 4

173 weeks to recover prior to resuming of behavioral training.

174

175   **Experimental tasks and behavioral stimuli**

176   All behavioral tasks, data collection and recording techniques have been

177   described previously (Marino et al. 2012a). Monkeys were seated in a primate chair with

178   their heads restrained for the duration of an experiment (1-3 hours). They faced a display

179   cathode ray tube monitor that provided an unobstructed view of the central visual area

180   50° x 60°. Extracellular recording was performed with tungsten microelectrodes (0.5-5

181   MΩ impedance, Frederick Haer) inserted through guide tubes (23 gauge) that were

182   anchored in delrin grids (Crist et al., 1988). Electrodes were advanced with a hydraulic

183   microdrive (Narishege M095) into the SC where we proceeded to isolate single neurons.

184   The monkeys were required to perform two blocked visually-guided saccade tasks

185   (Fig. 2A,B). Each trial required the monkeys to generate a single saccade from the

186   central fixation point (FP) to a peripheral visual target (T). At the start of each trial, the

187   screen turned black and after a period of 250 ms a circular grayscale FP of constant

188   luminance (0.25° diameter spot, 3.5cd/m^2) appeared at the center of the screen against a

189   black background (~0.0001 cd/m^2). Fixation of the FP was required for a variable period

190   (500 - 800 ms) until either a small circular 0.25º grayscale T appeared (delay task), or the

191   FP was extinguished (gap task). During the inter-trial interval (800-1500 ms duration),

192   the display screen was diffusely illuminated(0.5 cd/m^2) .

193   The delay task (Fig. 2A) was used to isolate and classify the visual and motor

194   response of each neuron. The delay period in this task temporally separated neural

195   activity that was related to the appearance of a visual target and the saccadic motor

196   response. In this task, the monkeys were required to continue fixating the FP for an

197   additional 500-800 ms after T appearance. Only after FP disappearance was the monkey

198   allowed to initiate a saccade to the T.

199   The gap task (Fig. 2B) was used to elicit pre-visual activity in the SC, reduce

200   SRT, and facilitate the production of express saccades. (Edelman and Keller 1996; Dorris

201   et al. 1997; Dorris and Munoz 1998; Sparks et al. 2000). In this task, monkeys were

202   required to make a saccade to the visual target immediately after its appearance. A 200

203   ms period of darkness (gap) was inserted into each trial between FP disappearance and T

204   appearance (Saslow 1967), which reduced SRT and facilitated generation of express

205   saccades (Fischer and Boch 1983; Fischer 1986; Fischer and Weber 1993). The 200ms

206   gap period imposes temporal predictability that may serve to shape the pre-saccadic

207   activity. During this gap period, the monkey was required to continue fixating the

208   location of the extinguished FP until the T appeared either in or opposite to the location

209   of each neuron's peak visual response field (RF). Response fields were mapped online

210   and targets were placed at the target location that yielded the greatest visual and/or motor

211   response (Marino et al. 2008). The monkeys were required to initiate a saccade to the T

212   within 1000ms of its appearance.

213   FP luminance was held constant at 3.5 cd/m^2 and seven distinct target luminance

214   levels (0.001 cd/m^2, 0.005 cd/m^2, 0.044 cd/m^2, 0.4 cd/m^2, 3.5 cd/m^2, 17.5 cd/m^2, and 42.5

215   cd/m^2) were randomly interleaved within each block of trials. Luminance was measured

216   with an optometer (UDT instruments, model S471) that was positioned directly against

217   the screen of the monitor and centered on the stimulus. After each correct trial the

218   monkey was rewarded with fruit juice or water. 10 to 20 correct trials per luminance

219   condition were recorded in the gap task and 6 to 10 trials per luminance condition were

220   recorded in the delay task.

221

222   **Neuron Analysis and Classification**

223   Trains of action potentials (averaged across all correct saccade trials to the same

224   target location) were convolved into spike density functions for each neuron using either

225   a Poisson kernal (growth constant = 1ms, decay constant = 20ms) (Thompson et al.

226   1996) or a Gaussian kernel (σ = 5ms) for each spike. A Poisson kernel was used to

227   calculate response onset times and pre-visual activity because it only implemented

228   temporal smoothing after each spike while the Gaussian kernel was used to calculate

229   peak responses because it calculated a balanced average of neural activity. Spike density

230   functions were aligned on target appearance in order to analyze visual responses and pre-

231   visual activity, and aligned on saccade onset when analyzing motor responses.

232   Neurons were classified based on their visual- or saccade-related responses in the

233   delay task when the T was placed at the peak location within their RF. Visual and

234   saccade related activity was classified relative to two specific baseline epoch periods

235   (Fig. 2A). Visual baseline activity was calculated as the average discharge from all

236   correct trials during the last 100 ms of active fixation of the FP prior to T appearance.

237   Saccade baseline activity was calculated from the average discharge from all correct trials

238   100-50ms prior to the onset of the saccade (Fig. 2A). A visual response was classified

239   based on an increase of target aligned activity (Gaussian kernel) greater than 50 spikes/s

240   above the visual baseline and significant by a non-parametric Rank Sum test ($p < 0.05$)

241   during the visual epoch (50-150ms after target appearance but prior to the saccade

242   epoch). A motor response (Gaussian kernel) was classified based on an increase activity

243   in the saccade epoch (+/- 10 ms around the onset of the saccade) that was greater than 50

244   spikes/s above both the visual and saccade baselines and significant by a non-parametric

245   Rank Sum test ($p < 0.05$). Saccade activity was required to exceed the saccade baseline (in

246   addition to the visual baseline) in order to ensure that any sustained tonic visual activity

247   related to the continued presence of the target in the delay task would not be misclassified

248   as motor related saccade activity. Based on these criteria we analyzed 46 visual only

249   (V_{ONLY}), 94 visual-motor (VM), and 6 motor only (M_{ONLY}) neurons across 3 monkeys.

250   A subset of the saccade-related neurons (VM and M) were further sub-classified

251   as buildup neurons based on whether or not they exhibited significant pre-visual activity

252   in the gap task after the disappearance of the FP but prior to the arrival of the visual

253   response in the SC (Munoz and Wurtz 1995). Neurons with buildup activity were

254   classified based on a significant increase in activity during the pre-visual epoch (10 to 40

255   ms after T appearance) relative to the visual baseline epoch (last 100ms of active fixation

256   prior to FP disappearance) (Fig. 2B). This ensured that buildup activity was measured

257   prior to the arrival of the target-related visual response in the SC (Marino et al. 2012a).

258   Significant buildup activity required that the activity in the pre-visual epoch be at least

259   15 spikes/s greater than the activity in the visual baseline epoch and significant by a non-

260   parametric Rank Sum test ($p < 0.05$). Based on these criteria, 31 of 94 VM neurons

261   exhibited buildup activity, all of the M_{ONLY} neurons (6 of 6) exhibited buildup activity,

262   and none of the V_{ONLY} neurons (0 of 46) exhibited significant buildup activity. Mean

263   population activity was calculated from the unnormalized spike density functions from all

264   neurons within the same classification group. Each neuron contributed a single trial-

265   averaged spike density function per condition and was weighted equally within the

266   calculated mean population activity.

267

268   **Behavioral Analyses**

269   Data were analyzed offline with custom Matlab (Matlab 7.4, Mathworks Inc)

270   software. The start and end of saccades were determined automatically from velocity and

271   acceleration criteria and then verified offline by the experimenter. To determine the

272   shortest SRT for visually-driven saccades, we compared the binned (5ms) SRT

273   distributions for correct (towards target) and direction error (opposite target) saccades in

274   the two target gap task. The shortest visually driven SRT latency was determined at each

275   target luminance as the earliest latency when correct saccades significantly outnumbered

276   direction errors (for details see Marino and Munoz 2009; Marino et al. 2012a).

277   Behavioral saccade data from monkey 3 was excluded from analysis due to the small

278   number of express saccades performed (mean 4.9% +/- 0.8% collapsed across luminance

279   conditions). All mean values reported also include the standard error of the mean unless

280   stated otherwise.

281

282   **Neuron Analyses**

283   The timing (visual response onset latency: VROL) and peak magnitude of the

284   initial phasic burst of the visual response were calculated at each target luminance level

285   in relation to express saccades for all neurons that had a significant visual response.

286   VROL was determined (relative to the time the target appeared) from target aligned spike

287   density functions (Poisson kernel) at each target luminance for each neuron. VROL was

288   defined as the onset of stable (at least 20ms) statistical significance ($p<0.05$) between the

289   mean activity during the visual baseline and a moving temporal window (1 ms resolution,

290   1ms increment) within the visual epoch (non-parametric Rank Sum test) (Fig. 2A).

291   Because VROL changed with target luminance, anticipatory saccade (saccades with

292   SRTs less than the luminance specific afferent visual delays) cut-off times were

293   calculated separately at each luminance specific VROL (for details see Marino et al.

294   2012).

295   The effect of luminance on the accumulated amount of buildup activity was

296   determined from the combined population of VM and M_{ONLY} neurons that exhibited

297   significant build-up activity.   This parameter was calculated from the summated area

298   under the curve of the target-aligned spike density function from target appearance until

299   10 ms prior to the mean luminance specific VROL (VROL occurred earlier with

300   increasing luminance) in the gap task. Both the VROL and accumulated buildup were

301   calculated using the Poisson function instead of a Gaussian function to ensure that each

302   luminance specific VROL was not artificially shifted earlier in time. The amounts of

303   accumulated buildup that was calculated at each luminance level were compared to each

304   other using a z test for proportions. All statistical comparisons were calculated with

305   repeated measures ANOVA with post hoc Bonferroni corrected pairwise comparisons

306   unless stated otherwise. All mean values reported also include the standard error of the

307   mean unless stated otherwise.

308   Express saccade ranges were defined independently at each target luminance

309   value from the timing of the corresponding VROL and shortest visually triggered SRTs.

310   We defined express saccades as visually triggered saccades where the visual response

311   was temporally merged with the motor response within VM neurons in the SCi. Because

312   there was no clear separation between the regular and express saccade latencies at several

313   target luminance levels, we estimated the express saccade range based upon the

314   neurophysiological responses.   The mean time difference between the VROL and the

315   shortest SRT bin (Fig. 3B) was 16.02 ms +/- 2.6 ms. Therefore we defined the express

316   saccade range as a 30 ms epoch beginning 15 ms after each luminance specific VROL in

317   the gap task. We chose this conservative 30ms epoch in order to help ensure that only

318   express saccades were included. This estimation of the express saccade range could be

319   subject to error if the regular and express saccade distributions significantly overlap

320   within the first 45ms of each luminance specific VROL.

321

322   **Expanded Express Saccade Model**

323   It was hypothesized that express saccades are generated when the visual response

324   and buildup activity in the SC sum together to cross a neural threshold and trigger a

325   saccade (Dorris et al. 1997; Dorris and Munoz 1998). In order to test this model, we

326   examined how changes to the combined peak visual response and accumulated buildup

327   activity at each luminance level affected the proportion of express saccades that were

328   produced. Since it is unclear how much of the pre-visual activity is temporally integrated

329   to influence the merged visual and motor response during express saccades, we

330   calculated pre-visual activity from both a long (cumulative buildup calculated from the

331   time of T appearance) and a short (instantaneous buildup calculated from an averaged

332   10ms window ending 10ms before the luminance specific VROL) temporal window. The

333   individual contributions of the peak visual response and cumulative buildup activity were

334   normalized and the proportion of express saccades produced was modelled as a linear

335   combination of each signal:

336                    $w_1(V_{peak})$ + $w_2(BU)$ = % Express Saccades Produced

337   where w_1 and w_2 are the strengths of the proportional weights of the normalized visual

338   peak response (V_{peak}) and buildup activity (BU). Values of w_1 and w_2 were calculated

339   that most closely matched the measured proportions of express saccades that were

340   produced at each luminance level. This enabled the model to predict the relative

341   importance of changes to the peak magnitude of the visual response relative to the

342   accumulated buildup activity in influencing the likelihood of producing an express

343   saccade.

344

345   **RESULTS**

346   **Target Luminance Modulated Express Saccade Latency**

347   We assessed the links between express saccade latency and neural response

348   latency by examining how the timing of neural visual responses and the shortest visually

349   triggered SRTs co-varied with target luminance. Figure 3A illustrates the effects of a

350   changing target luminance on the underlying SRT distribution and the corresponding

351   visual response in VM neurons. When target luminance was decreased toward detection

352   threshold (top traces), the VROL and peak of the visual response in VM neurons

353   occurred significantly later in time (Fig. 3A, Colored lines), and the earliest time for a

354   visually-triggered saccade (non-anticipatory) also occurred significantly later in time

355   (Fig. 3A, histogram: dotted black lines denote first bin in SRT distribution where

356   performance exceeds anticipatory chance, Binary sign test p<0.05). Figure 3B

357   summarizes the temporal changes to the visual and earliest SRT response as a function of

358   target luminance calculated from the mean of each recording session. As target

359   luminance increased, VROL and the time of peak visual response decreased. In addition,

360   the onset time of the express epoch also decreased. The mean time between each

361   luminance specific VROL and the earliest visually triggered SRT bin was 16ms +/-

362   2.7ms, whereas the mean time between each luminance specific peak visual response

363   time and earliest triggered SRT bin was -7.5ms +/- 2.8ms (SE). The time difference

364   between the means of the earliest visually-triggered SRT bin and the VROL were

365   significantly different (Bonferroni corrected pair-wise comparisons p > 0.05), except for

366   the 2 dimmest luminance levels (Bonferroni corrected pair-wise comparisons p < 0.05).

367   The time differences between the earliest visually-triggered SRT bin and the peak of the

368   visual response were not significantly different (Bonferroni corrected pair-wise

369   comparisons p > 0.05) at all but the 2 dimmest luminance levels (Bonferroni corrected

370   pair-wise comparisons p < 0.05). This suggests that at all but the dimmest target

371   luminance levels, a visually triggered saccade was not launched until the visual response

372   approached its peak level. The timing of both the neural visual response and fastest

373   visually triggered SRT co-varied with target luminance, suggesting that the

374   corresponding express saccade ranges were not fixed but instead varied systematically

375   with target luminance. The maximum difference between the fastest and slowest mean

376   VROL, time of peak visual response, and earliest visually triggered SRT was VROL:

377   90.6ms +/- 2.6 (SE); Peak Time: 92.4ms +/- 2.8ms (SE); SRT: 80 ms (Fig. 3A, difference

378   of bins), indicating that express saccade ranges were altered by more than 80ms across

379   the luminance ranges employed here. Furthermore, VROL was linearly related to and

380   highly correlated with both the peak time of the visual response (Fig. 3C; gray line: slope

381   = 1.05, r = 0.996, p<0.05) and the earliest SRT response time (Fig. 3C; black line: slope

382   = 0.93, r = 0.995, p<0.05).

383

384   **Target Luminance Modulated the Likelihood of Producing an Express Saccade**

385   In order to determine how target luminance modulated the likelihood of

386   producing an express saccade, we calculated the proportion of express saccades produced

387   within the 30 ms express saccade epoch (as determined by the timing of the VROL and

388   time of the earliest visually triggered SRT bin; See Methods). Figure 3D (gray line)

389   illustrates the percent of express saccades produced at each luminance level from the 2

390   monkeys that performed a significant number of express saccades. The curve formed an

391   inverted U-shaped function whereby the percent of express saccades increased from

392   0.001 cd/m^2 to 3.5 cd/m^2 (z test for proportions z=4.85, p<0.01), and then decreased from

393   3.5 cd/m^2 to 42.5cd/m^2 (z test for proportions z=6.88, p<0.01). Because our estimate of

394   the express saccade epoch did not account for possible overlap between regular and

395   express saccade distributions, the calculated proportion of express saccades may be

396   overestimated at target luminance levels below 3.5 cd/m^2 where the regular and express

397   saccade latency distribution modes are indistinctly separated (Fig. 3A).

398

399   **The Visual Responses of V$_{ONLY}$ Neurons were Unchanged during Express Saccades**

400   Visual neurons that lacked saccade responses are believed to reside in the SCs and

401   reflect earlier stages of visual processing relative to the SCi (Boehnke and Munoz 2008).

402   The model (Fig. 1) asserts that express saccades are triggered at the sensorimotor

403   integration level of the SCi; however, if express saccades are triggered earlier in the

404   sensory-to-motor transformation, then we would expect the earliest visual only responses

405   to be increased or altered during express saccades. In order to determine whether V_{ONLY}

406   signals were altered during the production of express saccades, we compared the V_{ONLY}

407   neuron population during express and regular latency saccades with a running t-test (Fig.

408   4). Neural population activity comparing regular and express saccades was calculated

409   separately at each target luminance condition. Neurons were only included within the

410   express saccade comparison population at a given luminance condition if both regular

411   and express saccade trials were elicited. There was no difference in the target aligned

412   population activity from the time of the visual response until more than 100ms after

413   response onset, indicating that the peak and duration of the initial visual response was

414   unchanged (5ms windows, t-test, p>0.05). (Fig. 4A). Furthermore there were no

415   consistent differences between express and regular saccades across the 7 different target

416   luminance conditions. When aligned on saccade onset (Fig. 4B), there was an increase in

417   activity immediately prior to the saccade (due to the visual response) at all luminances

418   above 0.4 cd/m^2 (5ms windows, t-test, p<0.05), except the brightest luminance where the

419   statistical significance of this difference dropped (p=0.13). At target luminances of

420   0.044cd/m^2 and below, the reduced visual response to the dim stimuli did not contribute

421   enough to separate the activity significantly between regular and express saccades (Fig.

422   4B). Therefore, V_{ONLY} neurons in the SCs do not contribute directly to express saccade

423   generation.

424

425 **Merging of Sensory and Motor Responses in VM Neurons During Express Saccades**

426   During an express saccade, the visual and motor responses of VM neurons in the

427 SCi merge (Edelman and Keller 1996; Dorris et al. 1997; Sparks et al. 2000). In order to

428 examine how merged visuomotor responses differed from temporally separated visual

429 responses during regular-latency saccades, we compared the visual and motor responses

430 of VM neurons during express and regular-latency saccades using a running t-test (Fig. 5,

431 overlapping black asterisks). When aligned to target appearance (Fig. 5A), express

432 saccades were accompanied by increased pre-visual activity as well increased activity

433 immediately after the peak of the visual response. When aligned on saccade onset (Fig.

434 5B), express saccades had increased activity immediately prior to saccade initiation at all

435 luminances above 0.044 cd/m^2.

436

437 **Target Luminance Impacts Peak Visual Response and Accumulated Buildup**

438 **Activity**

439   Increases in both buildup activity (Dorris et al. 1997; Dorris and Munoz 1998)

440 and visual response magnitude (Marino et al. 2012a) in SCi neurons correlate with SRT

441 and express saccade production. However, a reciprocal relationship may exist whereby

442 the delayed onset of visual responses to dimmer stimuli may allow additional time for

443 pre-visual activity to accumulate. Such a reciprocal relationship could influence the

444 likelihood of crossing the saccade threshold and generating an express saccade. In order

445 to examine this relationship in detail, we calculated the luminance dependant changes to

446 buildup activity and visual response magnitude in the SCi during the gap task.

447   Figure 6A,C illustrates the effect of target luminance on the magnitude of the

448   visual response. Only VM neurons with no significant buildup activity (N = 63 neurons;

449   See Methods) were used for this calculation to avoid contamination by buildup activity.

450   There was a main effect of luminance on the peak of the visual response (*Peak*

451   *Magnitude: (gap)* $F(6,654) = 102.9$, $P < 0.01$). As luminance was increased from 0.001

452   cd/m^2 to 42.5 cd/m^2, the VROL occurred earlier and had a higher peak (Fig. 6A). Figure

453   6C illustrates the mean of the peak visual response at each luminance level for the 63 VM

454   neurons without buildup activity. As luminance increased from 0.001 to 0.4 cd/m^2, the

455   mean peak visual response increased (Bonferroni corrected pair-wise comparisons $p <$

456   0.05). Above 0.4 cd/m^2 the trend of the peak visual response increased, however these

457   increases were not significant ($p>0.05$).

458   Figure 6B,D illustrates the effect of target luminance on buildup activity from the

459   combined population of all VM and M_{ONLY} neurons with buildup activity (See Methods).

460   When the onset of the visual response was delayed for dimmer target stimuli, the amount

461   of pre-visual activity increased (Fig. 6B). Figure 6D illustrates the effect of target

462   luminance on pre-visual activity among neurons with buildup activity. Pre-visual activity

463   started to increase during the gap period and continued to increase until the onset of the

464   visual response (Fig. 6B). It is unclear how much of the pre-visual activity is temporally

465   integrated to influence the merged visual and motor response during express saccades.

466   Because of this uncertainty, we calculated pre-visual activity from both a long

467   (cumulative buildup calculated from the time of T appearance) and a short (instantaneous

468   buildup calculated from an averaged 10ms window ending 10ms before the luminance

469   specific VROL) temporal window. As target luminance increased, both the cumulative

470   and the instantaneous pre-visual activity measures decreased with increasing target

471   luminance (Fig. 6D).

472

473   **Predicting Express Saccades From Neural Parameters**

474   Previous studies (Dorris et al. 1997; Dorris and Munoz 1998) have suggested that

475   both the visual response and buildup activity combine to influence express saccade

476   generation (Fig. 1). However, it is unclear what the relative influence of these neural

477   parameters is, or whether they alone are sufficient to predict express saccades. In order

478   to address this question, we fit a linear model to the data that calculated a weighted

479   combination of each neural parameter (peak visual response and buildup activity) that

480   best fit the calculated likelihood of producing an express saccade at each of the 7 target

481   luminance levels tested (See Methods). The resulting weightings of the visual peak and

482   accumulated buildup parameters provided evidence as to which signal most strongly

483   influenced express saccade production.

484   Figure 7A illustrates the sum of squares error (SSE) of the best model fits of

485   physiologically derived parameters to the calculated express saccade likelihood at each

486   experimental target luminance level. Both the cumulative (white bars) and instantaneous

487   buildup activity were independently calculated and modelled separately (see methods).

488   We used a bootstrapping method to inform the statistical significance of SSE

489   comparisons. Bootstrapping of the best fits of the express saccade proportions to neural

490   parameters were calculated from a random sampling (with replacement) of the 7

491   experimental luminance levels with 10000 repetitions. The resulting bootstrapped SSEs

492   were normally distributed (Kolmogorov-Smirnov test p < 0.01) and non-overlapping 95%

493   confidence intervals (CI) were used to determine statistically significant differences.

494   Using this statistical method, when two parameters (peak and build-up) were assessed

495   (Fig. 7A left side), there was a significantly reduced SSE (non-overlapping CI in

496   bootstrapped comparisons) when instantaneous build-up was used compared to

497   cumulative build-up. Overall, the linear combination of the peak visual response and

498   buildup alone could not account well for express saccade likelihood and yielded a high

499   SSE (Fig. 7A left side). This remaining error suggested that additional parameters are

500   required.

501   When express saccades occurred, we observed an increase in activity in all VM

502   and V only neurons immediately prior to (~30ms) saccade onset (Fig. 4B, 5B overlapping

503   black asterisks denote significant differences). This significant increase in activity

504   immediately prior to the saccade was not present when target luminance levels were

505   below $0.4cd/m^2$, and it decreased in duration at the brightest target luminance level (42.5

506   cd/m^2). Because this pattern was consistent with the observed decrease in express

507   saccades at the brightest luminances (Fig. 3D), we added cumulative pre-saccadic

508   activity from VM and V-only neurons (Fig. 4B, 5B) as additional parameters to the

509   model. Cumulative pre-saccadic activity was calculated from the cumulative difference

510   between the saccade aligned activity of V and VM neurons during regular and express

511   saccades. These cumulative differences were only calculated when the activity between

512   regular and express saccades were significantly different (Fig 4B, 5B overlapping black

513   asterisks) over the 30ms temporal window immediately prior to saccade onset. We also

514   examined VROL as an additional physiological parameter in the model to determine

515   whether it improved the model's ability to predict of express saccade likelihood.

516   When three parameters were tested (Fig. 7A right side), the addition of pre-

517 saccadic activity from VM neurons yielded the lowest SSE and yielded a model fit that

518 was significantly better than VROL or pre-saccadic activity from V-only neurons at

519 predicting express saccades regardless of whether the cumulative (Fig. 7A white bars) or

520 instantaneous build-up (Fig. 7A grey bars) was used (non-overlapping CI in bootstrapped

521 comparisons). The difference in SSE between instantaneous and cumulative build-up was

522 significant in all the two and three parameter model fits with the exception of the lowest

523 error condition where pre-saccadic activity from VM neurons was included (non-

524 overlapping CI in bootstrapped comparisons).

525   The modelled best fits resulted in calculated weights for each combination of

526 neural parameters (Fig. 7B). In both the two and three parameter case, instantaneous

527 build-up was weighted higher than cumulative build up. This indicates that build-up

528 activity is most predictive of express saccades then when it is sampled immediately prior

529 to the visual response. When three parameters were modelled (Fig. 7B right panel), the

530 peak visual response and build-up were weighted more strongly than pre-saccadic

531 activity from VM neurons. This suggests that these two parameters still have the

532 strongest influence on whether an express saccade is generated.   Figure 7C illustrates the

533 best model fits (grey solid and dashed lines) to the measured express saccade behavior

534 (Fig. 7C black solid line). Only the three parameter model that combines the peak visual

535 response, instantaneous build-up, and pre-saccadic activity is best able to reflect the

536 decreasing trend in express saccades at the highest target luminance levels.

537

538 **DISCUSSION**

539   Here, we have shown that the latency and likelihood of producing express

540   saccades was dependent on the properties of the visual stimulus. Specifically, target

541   luminance altered the timing and magnitude of visual responses in the SC. In addition,

542   changes to the timing of the visual response also altered the amount of accumulated

543   buildup activity in the SCi. These modulations to the visual response and buildup activity

544   combined to influence express saccade latency and likelihood. Altered stimulus

545   luminance and contrast has been shown previously to affect retinal transduction times

546   (Lennie 1981; Barbur et al. 1998), as well as the timing and magnitude of visual

547   responses in the SC (Bell et al. 2006; Marino et al. 2012a), lateral intraparietal area

548   (Tanaka et al. 2013), primary visual cortex (Gawne 2000), and V4 (Lee et al. 2007). As a

549   consequence, at dimmer luminance levels (< 0.044 cd/m^2) a smaller proportion of express

550   saccades were generated at significantly slower latencies (130-160 ms) and with less

551   bimodality in the underlying distribution than traditionally reported.

552   Based on our observations, we propose an expanded definition for express

553   saccades that does not require bimodality in the underlying SRT distribution and does not

554   involve an absolute latency range. As target luminance decreased, the separation between

555   the regular and express saccade modes within SRT distributions correspondingly

556   decreased until they merged together (below 0.4cd/m^2). Because we defined express

557   saccades as being temporally linked to the timing of the visual response in the SCi, and

558   the visual responses were delayed at dimmer luminance levels, we observed express

559   saccades at longer latencies even when no bimodality was evident in the SRT distribution

560   (i.e., at luminance levels below 0.044 cd/m^2, Fig. 3A). This result suggests that the

561   neural mechanisms underlying express saccade generation are highly sensitive to external

562 stimulus properties like luminance. Furthermore, express saccades can only be accurately

563 dissociated from regular saccades when the timing of the visual response in the SCi is

564 known. This issue is especially relevant for clinical behavioral studies of saccades where

565 the specific temporal parameters of the visual response are not usually measured or taken

566 into account when analyzing express or shorter latency saccades (Fischer 1986; Carpenter

567 2001; Munoz et al. 2003; Chan et al. 2005; Dickov and Morrison 2006).

568

569 **Influences of Pre-visual Activity on Express Saccades**

570   It has been previously shown that the amount of buildup activity in the SCi

571 correlated with saccade latency and that this enhanced discharge strongly predicted when

572 an express saccade will be generated (Dorris et al. 1997). The amount of buildup activity

573 can be modulated by internally-driven factors such as target predictability (Basso and

574 Wurtz 1997; Dorris and Munoz 1998; Basso and Wurtz 1998) and the expected value of

575 saccadic goals (Milstein and Dorris 2007). In our study, pre-visual activity was

576 manipulated by purely sensory mechanisms that delayed when the visual response arrived

577 in the SCi, thus impacting the time available for pre-visual activity to accumulate. We

578 observed a reciprocal relationship between the timing of the visual response and the

579 accumulated amount of buildup activity present in the SCi prior to saccades. Specifically,

580 delayed visual responses to dimmer stimuli resulted in additional time for buildup activity

581 to accumulate. This increased buildup at lower luminance levels likely helped to

582 facilitate the reduced proportion of express saccades that we observed. Without this

583 increased buildup, it is unlikely that the reduced visual response at lower luminance

584 levels would enable any express saccades to be triggered at all. Evidence from a human

585   express saccade study (Rolfs and Vitu 2007) suggests that saccade metrics are computed

586   before the target is displayed, which further highlights the importance of advanced motor

587   preparation for express saccade production.

588

589   **Influences of the Visual Response on Express Saccades**

590   Several stimulus-driven factors influence express saccades. For example, when

591   multiple distant visual targets abruptly appear during visual search tasks where an oddball

592   target is presented amongst distractors, express saccades are almost never made (McPeek

593   and Schiller 1994; Weber and Fischer 1994). However, express saccades can be elicited

594   during scanning tasks when multiple stable objects are present, but an abrupt appearance

595   of a single target at an anticipated location is still required (Sommer 1994; Sommer

596   1997). When multiple targets appear abruptly, express saccades tend to only be made if:

597   1) a temporal asynchrony is introduced to the time the targets appear (Schiller et al.

598   2004), or 2) if only 2 targets are presented within close spatial proximity (i.e., within 45°

599   of visual angle from each other) (Edelman and Keller 1996; Edelman and Keller 1998).

600   When visual targets are presented in close proximity, the corresponding activity on the

601   SC sensory-motor map for nearby visual targets will likely overlap (Edelman and Keller

602   1998; Anderson et al. 1998; Marino et al. 2012b) forming a single hill of activity on the

603   SC map rather than multiple competing ones.

604   Here, we have demonstrated that target luminance is an important factor that

605   influences the express saccade generating mechanism by determining when and how

606   often express saccades are made. Luminance also impacts the influence of prediction

607   because changes to the timing of the visual transient allowed more buildup activity to

608 accumulate and influence saccade generation. This study further extends previous studies

609 whereby Boch and colleagues (Boch et al. 1984) observed a decrease in express saccades

610 with decreasing luminance, and Weber and colleagues (Weber et al. 1991) did not show

611 any effect of luminance contrast on the proportion of express saccades generated.

612 However as we have discussed, without insight into the corresponding modulations to the

613 visual response, it is difficult to interpret their negative result. This highlights the

614 importance of understanding how altered stimulus properties affect the timing and

615 magnitude of visual responses in the SCi before predictions or explanations can be made

616 as to how it impacts saccade performance.

617

618 **Express Saccades without SRT Distribution Bimodality**

619   Express saccades were first defined by the earliest distinct mode present within a

620 multimodal SRT distribution (Fischer and Boch 1983; Fischer 1986). However, the SRT

621 distributions (Fig. 3A) only demonstrate clear bimodality at the brightest luminance

622 levels employed. This bimodality gradually merged into a single mode when luminance

623 levels decreased toward detection threshold. However, if an express saccade was not

624 defined by bimodality, but instead by the temporal merging of visual and saccade motor

625 responses in the SCi (Fig. 1), then the poorly separated or single modes within the SRT

626 distributions for dimmer luminance levels still contained a proportion of express

627 saccades.

628   When regular and express saccade distributions temporally merge, the extent to

629 which they overlap is unclear. The potential for overlap poses a significant challenge for

630 dissociating between regular and express saccades at both the neural and behavioral level.

631   In this study, we addressed this problem by characterizing express saccades around a

632   narrow 30ms window that was constrained by afferent sensory response delays in the SC.

633   However, such an approach can only estimate express saccade latencies as it does not

634   account for potentially overlapping regular saccades in the same range. This approach

635   can potentially result in overestimation wherever overlap exists, and may account for the

636   decreases in express saccades below 3.5 cd/m^2 that we observed (Fig. 3D).

637

638   **Expanding Express Saccade Models**

639   Previous models of express saccade generation have hypothesized that an express

640   saccade is generated when the visual response is sufficiently large enough to exceed a

641   neural threshold and generate a saccade (Edelman and Keller 1996). This idea was further

642   developed by Dorris and colleagues (Dorris et al. 1997; Dorris and Munoz 1998) who

643   suggested that it was the combination of both pre-visual activity and the visual response

644   that must cross a neural threshold to trigger the saccade. Based on our results, we

645   propose a further extension of this model (Fig. 8) whereby express saccades generated to

646   high luminance stimuli are more strongly influenced by larger visual responses in the

647   SCi. However, for dimmer stimuli that approach detection thresholds, express saccades

648   have longer SRTs, but can still be generated despite a significantly reduced visual

649   response because of the additional accumulation of buildup activity (Fig. 4, 6B).

650   Although it may at first seem puzzling that the visual responses of

651   V$_{ONLY}$ SC neurons are not different during express saccades given that the "visual grasp

652   reflex" (Hess et al. 1946) is believed to bypass higher order cortical decisions and

653   transform visual responses into saccadic commands (Edelman and Keller 1996; Dorris et

654   al. 1997; Sparks et al. 2000). However, this seemingly counter-intuitive result can be

655   reconciled via a neural gate implemented downstream of the V_{ONLY} neurons that could

656   control whether an express saccade is triggered from the visual response. Isa and

657   colleagues have theorized such a neural gate between the visual only superficial and

658   visual-motor intermediate and deeper layers of the SC that controls express saccades (Isa

659   2002; Phongphanphanee et al. 2008). This theory suggests that an express saccade is only

660   triggered when the gate is closed and the visual response is directly propagated from the

661   SCs to the SCi to trigger the saccade (Isa 2002). Our results show that during express

662   saccades, the visual response increases in VM neurons (Fig. 5A) but stays the same in

663   V_{ONLY} neurons (Fig. 4A). Thus, our results are not inconsistent with this gating

664   mechanism which may exist between SCs and SCi, where express and regular saccadic

665   signals diverge.

666

667   **Other Neural Parameters Influencing Express Saccades**

668   The combined modulations of the peak visual response and accumulated buildup

669   activity could only account for increases in the proportion of express saccades at target

670   luminance levels below 3.5 cd/m^2. Above this luminance level, changes to the visual peak

671   or buildup activity could not account for the decrease in express saccades with increasing

672   target luminance that we observed (Fig. 7 A,B). By adding the cumulative pre-saccadic

673   activity of VM neurons during express saccades we accounted for more of the behavioral

674   data, however not all of the proportion of express saccade behavior was accounted for,

675   indicating that additional neural mechanisms likely contribute.

676   One factor that may also influence express saccade generation is the fixation-

677   related activity located in the rostral pole of the SCi (Munoz and Wurtz 1993a; Munoz

678   and Wurtz 1993b; Dorris and Munoz 1995; Everling et al. 1999). Neurons in the rostral

679   SCi have enhanced tonic discharge during active visual fixation which is hypothesized to

680   aid in anchoring gaze and inhibiting unwanted saccades (Munoz and Wurtz 1993a;

681   Munoz and Wurtz 1993b; Everling et al. 1999; Krauzlis 2005). During the gap period,

682   fixation-related activity in the SCi decreases (Dorris and Munoz 1995; Dorris et al. 1997;

683   Everling et al. 1999) and this decrease co-varies with mean SRT when the gap duration is

684   varied (Dorris and Munoz 1995). However when the gap duration remains constant, the

685   rate of decrease of fixation activity is largely invariant and does not correlate with inter-

686   trial variations in SRT including express saccades (Dorris et al. 1997). This evidence

687   suggests that decreases in fixation activity can only influence SRT (either directly or

688   indirectly) when external stimulus properties (related to the timing of the visual response

689   relative to the disappearance of the fixation point) are altered. As luminance increases,

690   the visual response occurs earlier and allows less time for fixation related activity to

691   decrease and disinhibit the rest of the SC. A recent study of express saccades in humans

692   supports this hypothesis because it was found that express saccades increase when

693   fixation disengagement is facilitated (Bibi and Edelman 2009).

694

695   Another possible factor that may influence express saccade generation is the area

696   or size of the visual or motor population response (i.e., point image) within the

697   topographic SC map (McIlwain 1986; Marino et al. 2008; Marino et al. 2012b). This

698   point image is believed to be shaped by nigral inhibition (Hikosaka and Wurtz 1983) and

699   lateral interactions within the SC itself (i.e., local excitation and distal inhibition)

700   (Munoz and Istvan 1998; Trappenberg et al. 2001; Dorris et al. 2007) that have been

701   shown to differ between SCs and SCi. The SCs exhibits stronger lateral inhibition than

702   the SCi (Phongphanphanee et al. 2014), which suggests that the SCs is more optimized

703   for localizing stimuli, while the SCi is more suitable for implementing an accumulating

704   saccadic decision signal with cortical and basal ganglia influence (Fig. 1).

705   We have shown previously that the size of the visual point image in the SC

706   changes with luminance (Marino et al. 2007). Furthermore, we used a neural field model

707   of lateral interactions within the SCi to predict that changes to the size of visual point

708   images significantly affected SRT such that increases in point image area decreased and

709   then increased SRT (Marino et al. 2012b). This is because increases in point image size

710   will decrease SRT until the point image grows beyond the hypothesized spatial extent of

711   local excitation and into regions of distal inhibition in the SC which slows SRT. We

712   therefore hypothesize that the reduction in the proportion of express saccades above 3.5

713   cd/m^2 could result from larger visual response point images in the SCi that may inhibit

714   the express saccade mechanism. Further study of the relationship between the spatial

715   extent of point images and their influence on saccades is needed to address this

716   possibility.

717

718   **Model Limitations**

719   Here we have proposed a neurophysiological definition of express saccades that

720   includes all visually triggered saccades that are coincident with the early part of the visual

721   response to an abruptly appearing visual target. It is also possible; however, that express

722 saccades involve other mechanisms that might better account for the overlapping of SRT

723 distributions and the reduction of the visual responses to different types of target stimuli

724 when describing regular and express latency saccades. Future investigations will have to

725 address such problems in order to improve the accuracy of separating regular and express

726 saccades when they overlap in order to improve the description of the underlying neural

727 mechanisms.

728

729 **Conclusions**

730   Express saccades represent the fastest and most direct sensory to motor

731 transformation in the visual system. The neural mechanisms underlying their generation

732 do not function at a fixed temporal latency but instead are strongly linked to the qualities

733 (timing, magnitude) of the visual response which can be modified by the external

734 properties of the stimulus. Therefore, the likelihood of producing an express saccade is

735 not only depended on advanced motor preparation but is also strongly influenced by

736 visual stimulus properties.

737

738

739   **FIGURE LEGENDS**

740   **Figure 1.** Conceptual neural model of express saccade generation based on trigger

741   thresholds in the SCi. **1A**, Spiking activity from a visual-motor SCi neuron during a

742   regular (blue lines) and express (red lines) latency saccade. Each vertical line represents a

743   single action potential. **1B**, Spikes expressed as a continuous spike density function. An

744   express saccade is triggered when the combined pre-visual activity (dashed red line)

745   visual response (solid red line) cross a neural threshold (dotted grey line) to trigger an

746   express saccade (Edelman and Keller 1996; Dorris and Munoz 1998). When this

747   combined response does not cross threshold, a regular latency saccade can be triggered at

748   a later time by a separate and distinct motor response (blue line).

749

750   **Figure 2.** Schematic representation of temporal events in the delay (**A**) and gap (**B**) tasks

751   for the fixation point (FP), target (T) and eye position (EYE). Vertical gray bars denote

752   key analysis epochs used to classify responses and neurons.

753

754   **Figure 3.** Effects of target luminance on express saccades and SC responses in the gap

755   task. (**A**) Relationship between express saccades and visual response latencies. Grey bars

756   denote a histogram of SRTs for correct saccades (above the zero line) and direction error

757   saccades (below the zero line) in the gap task across 7 different luminance levels (column

758   is organized from top to bottom in ascending luminance). The colored lines denote the

759   population activity of 63 VM neurons at each target luminance level in the gap task.

760   Population spike densities (Poisson Kernel) are aligned on target appearance and include

761   all correct trials (luminance specific visually triggered latencies) toward their optimal

762   location. Dotted lines denote earliest SRT bin where saccades are visually triggered.

763   Shaded SRT bins denote express saccade epoch derived from a combination of visual

764   response timing and earliest visually triggered SRT (see Methods). (**B**) Temporal

765   modulation of visual response properties (time of visual response onset latency and peak)

766   and the earliest visually triggered saccade latency (first histogram bin when saccade

767   performance exceeds chance). The onset and peak of the visual response are denoted by

768   solid and dotted grey lines respectively. The time of the first correct SRT bin is denoted

769   by a solid black line. (**C**) Linear correlations between VROL and the peak time of the

770   visual response (gray data points and line) and VROL and the earliest SRT response time

771   (black data points and line). (**D**). The mean proportion of express saccades across

772   monkeys 1 and 2 determined by the timing of the visual response properties and earliest

773   visually triggered SRT latencies.

774

775   **Figure 4.** Neural population spike density functions (Gaussian kernel σ = 5ms)

776   comparing regular (solid line) and express saccades (dotted lines) for all visual-only

777   neurons (Vs). Population spike densities are aligned on target appearance **4A** and saccade

778   onset **4B** and include all correct trials toward their optimal location in the gap task.

779   Express saccades were separated based on luminance specific ranges (see methods).

780   Colored lines denote the population response at each target luminance level (red: 42.5

781   cd/m^2, orange 17.5 cd/m^2, green 3.5 cd/m^2, dark blue 0.4 cd/m^2, cyan 0.044 cd/m^2, pink

782   0.005 cd/m^2, black 0.001 cd/m^2). The width of the colored background shading denotes

783   the standard error of the mean. Shaded vertical bars denote the time of the saccade (**4B**).

784   Overlapping black asterisks (top of each subpanel) denote times when the activity for

785   express saccades and regular saccades were significantly different (5ms window, t-test,

786   p<0.05).

787

788   **Figure 5.** Neural population spike density functions (Gaussian kernel σ = 5ms)

789   comparing regular (solid line) and express saccades (dotted lines) in visual-motor

790   neurons (VMs). Express saccades were separated based on luminance specific ranges (see

791   methods). Population spike densities are aligned on target appearance **5A** and saccade

792   onset **5B** and include all correct trials toward their optimal location in the gap task.

793   Colored lines denote the population response at each target luminance level (red: 42.5

794   cd/m^2, orange 17.5 cd/m^2, green 3.5 cd/m^2, dark blue 0.4 cd/m^2, cyan 0.044 cd/m^2, pink

795   0.005 cd/m^2, black 0.001 cd/m^2). The width of the colored background shading denotes

796   the standard error of the mean. Shaded vertical bars denote the pre-visual epoch and time

797   of visual peak (**5A**), and the pre-saccade epoch (**5B**). Overlapping black asterisks (top of

798   each subpanel) denote times when the activity for express saccades and regular saccades

799   were significantly different (5ms window, t-test, p<0.05).

800

801   **Figure 6. A-D.** Population spike density functions (Gaussian kernel σ = 5ms) from VMs

802   without buildup (**A**) and from all neurons with buildup (VMs and Ms) (**B**) aligned on

803   target appearance in the gap task. Colored lines denote the population response at each

804   target luminance level (red: 42.5 cd/m^2, orange 17.5 cd/m^2, green 3.5 cd/m^2, dark blue 0.4

805   cd/m^2, cyan 0.044 cd/m^2, pink 0.005 cd/m^2, black 0.001 cd/m^2). **C,D** Mean peak visual

806   response (**C**) and buildup activity (**D**) for each luminance level. Buildup activity was

807   calculated seperately as both the instantaneous buildup prior to the visual response (grey

808   line) and the cumulative buildup (black line).

809

810   **Figure 7.** Model predicting express saccade likelihood from SC response parameters. **A**.

811   Sum of squares error (SSE) from best model fits to the mean proportion of express

812   saccades produced across target luminance levels. Cumulative (white bars) and

813   instantaneous (grey bars) build-up were calculated and modelled separately. Separate

814   model fits were calculated from different combinations of neural parameters in the SC.

815   Parameters modeled included the peak of the visual response (Peak), instantaneous build-

816   up (BU), cumulative build-up (BU), and pre-saccadic (Pre-Sac) activity from VM and V

817   only neurons. **B**. The calculated parameter weights for the 2 and 3 parameter best fit

818   models. **C**. Best model fits to 2 and 3 parameter combinations of SC activity to the

819   measured express saccade likelihood at each target luminance level: 1) cumulative

820   buildup and peak visual response (light grey solid line), 2) instantaneous buildup and

821   peak visual response (grey dash-dotted line), and 3) cumulative buildup, peak visual

822   response and pre-saccadic activity (dark grey dotted line).

823

824   **Figure 8.** Our proposed extension of the pre-existing express saccade model whereby

825   bright stimuli trigger early express saccades (red line) and dim stimuli trigger later

826   express saccades (orange line). During express saccades, the merged visual and motor

827   responses produce an elongated visual response that triggers an express saccade when

828   this activity is accumulated and integrated. In this model early express saccades are more

829   prevalent because bright stimuli elicit larger visual responses. A reduced proportion of

830   late express saccades can still be triggered despite a significantly reduced visual response

831   because of the extra buildup activity that can accumulate.

832

833

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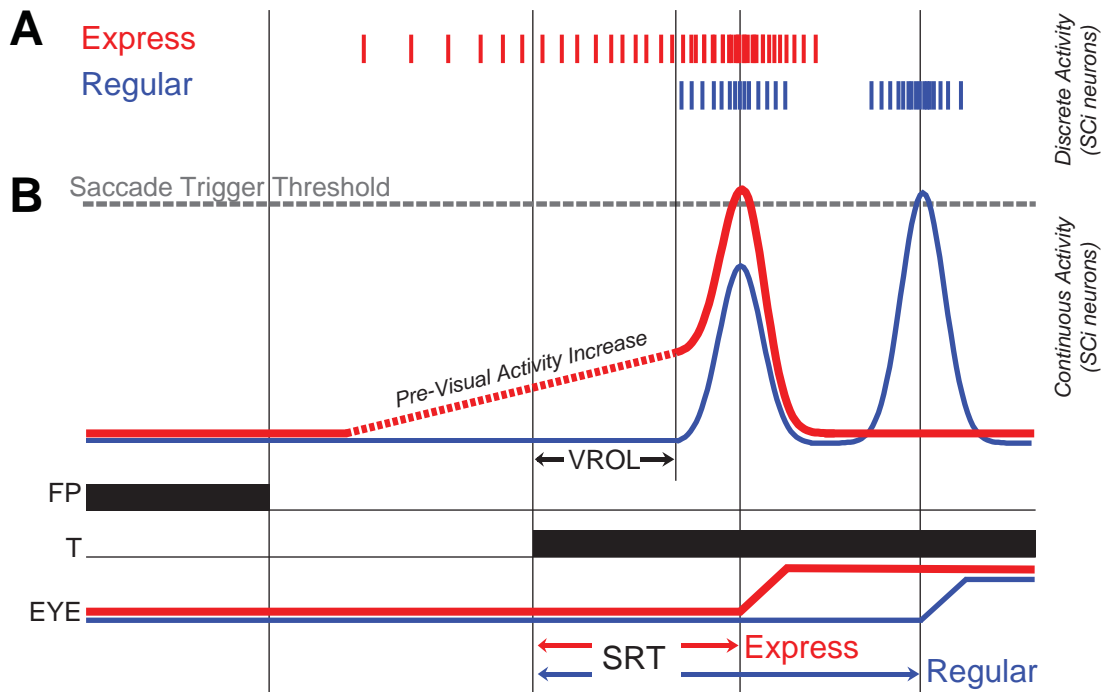945 *Neurophysiol* 76: 3666-3681, 1996.

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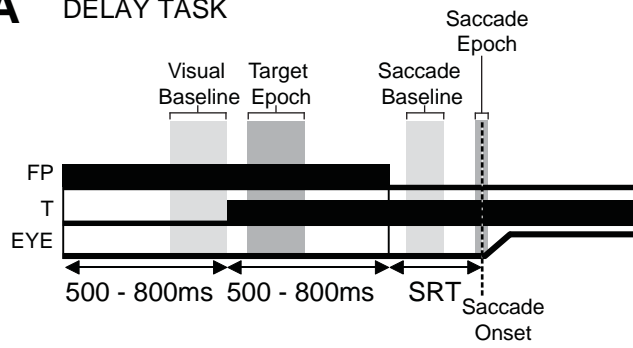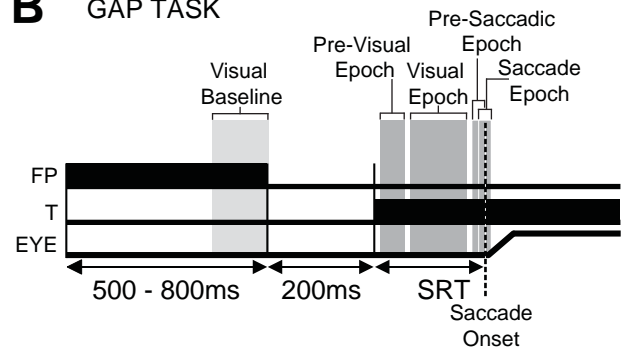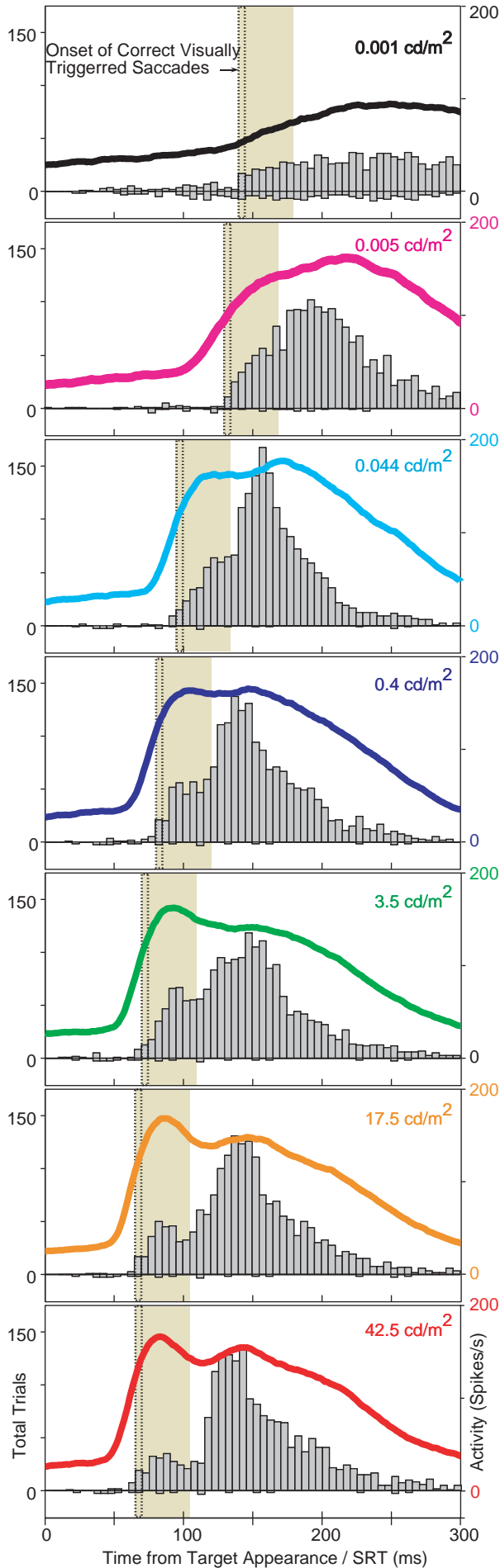
987

Established Express Saccade Model

A Express
   Regular

B Saccade Trigger Threshold

Pre-Visual Activity Increase

VROL

FP

T

EYE

SRT   Express

Regular

Discrete Activity (SCi neurons)

Continuous Activity (SCi neurons)

Marino et al. Fig. 1

A DELAY TASK

Visual Baseline
Target Epoch
Saccade Baseline
Saccade Epoch

FP
T
EYE

500 - 800ms 500 - 800ms SRT
Saccade Onset

B GAP TASK

Visual Baseline
Pre-Visual Epoch
Pre-Saccadic Epoch
Visual Epoch
Saccade Epoch

FP
T
EYE

500 - 800ms 200ms SRT
Saccade Onset

Marino et al. Fig. 2

A SRT Behavior and Visual-Motor Neuron Population

0.001 cd/m²

Onset of Correct Visually Triggered Saccades

0.005 cd/m²

0.044 cd/m²

0.4 cd/m²

3.5 cd/m²

17.5 cd/m²

42.5 cd/m²

Total Trials

Activity (Spikes/s)

Time from Target Appearance / SRT (ms)

B Timing of Visual Response and Saccade Behavior

Time (ms)

- - - Visual Peak
—— First Correct SRT BIN
—— VROL

Target Luminance (cd/m²)
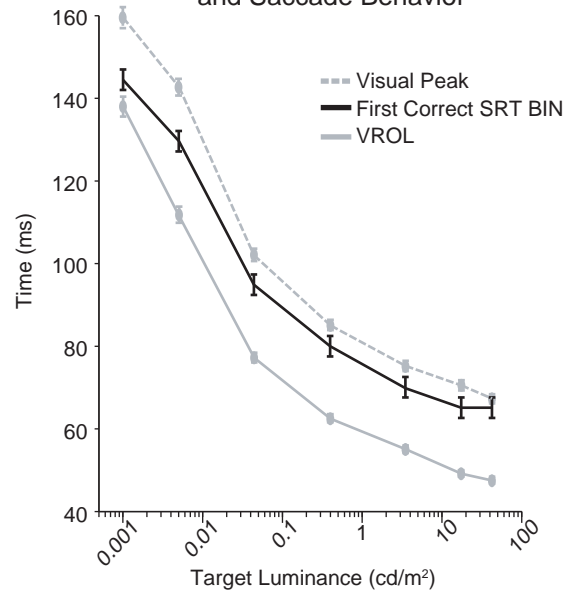
C Earliest Correct Behavior versus Visual Response

Time of First Correct SRT BIN (ms)

Time of Peak Visual Response (ms)

slope = 1.05
r=0.996

slope = 0.93
r = 0.995

VROL (ms)

D Proportion of Express Saccades

% Express Saccades

Target Luminance (cd/m²)
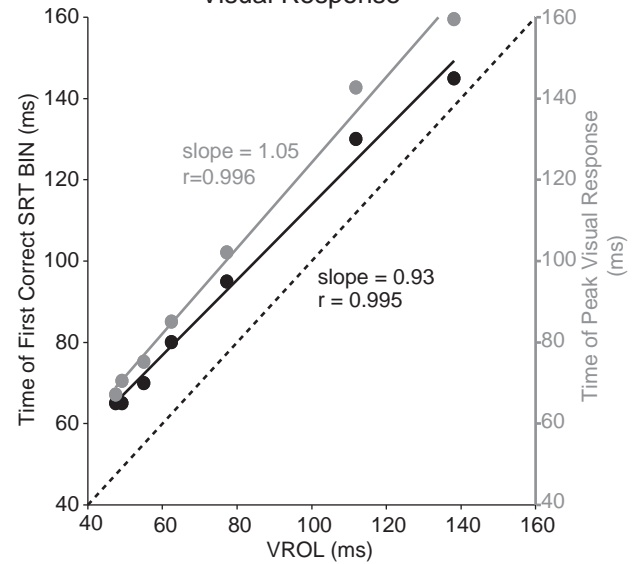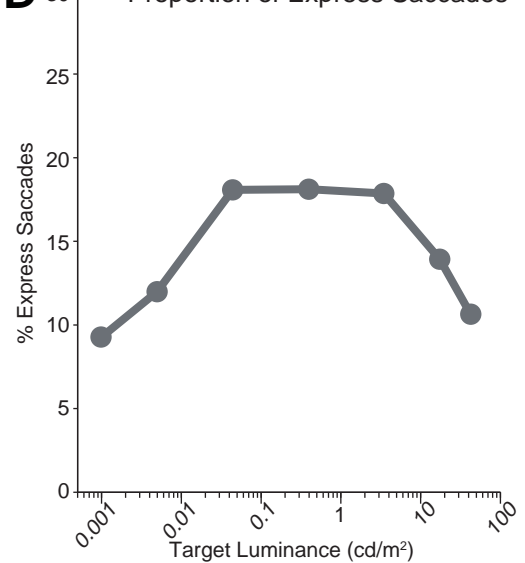
Marino et al. Fig. 3

Express Vs Regular Saccades (V Only Neurons)
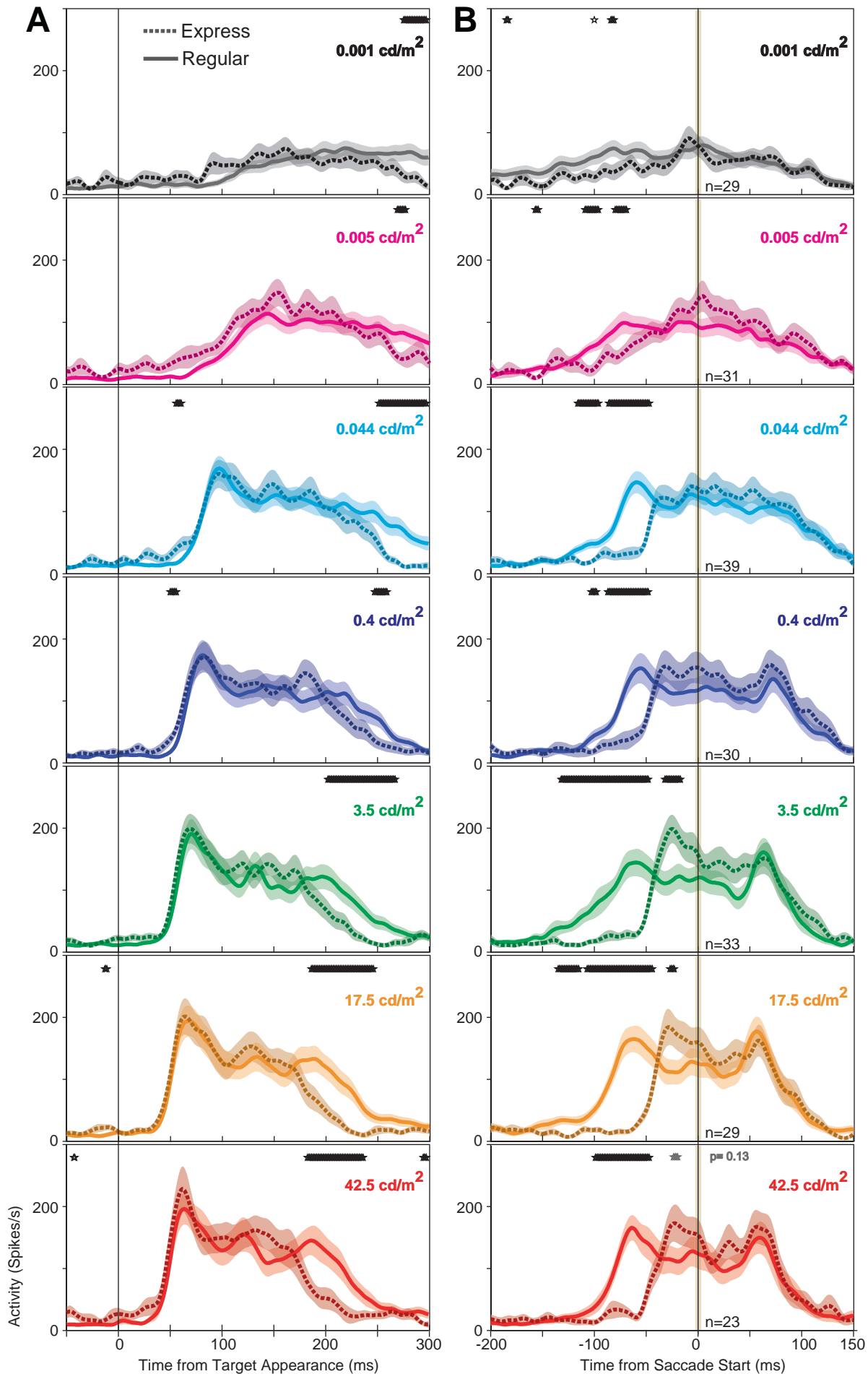
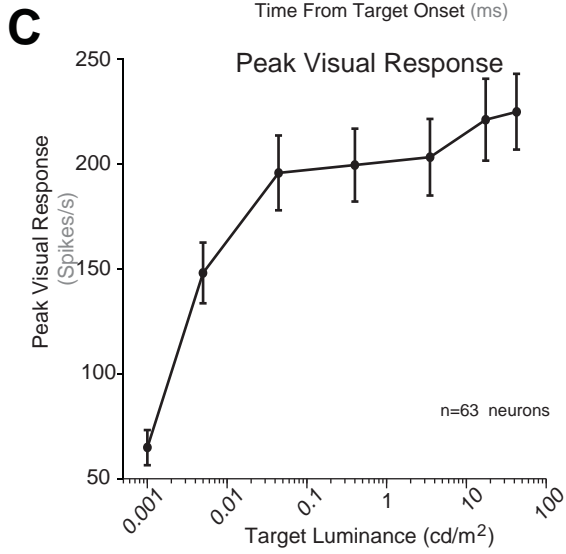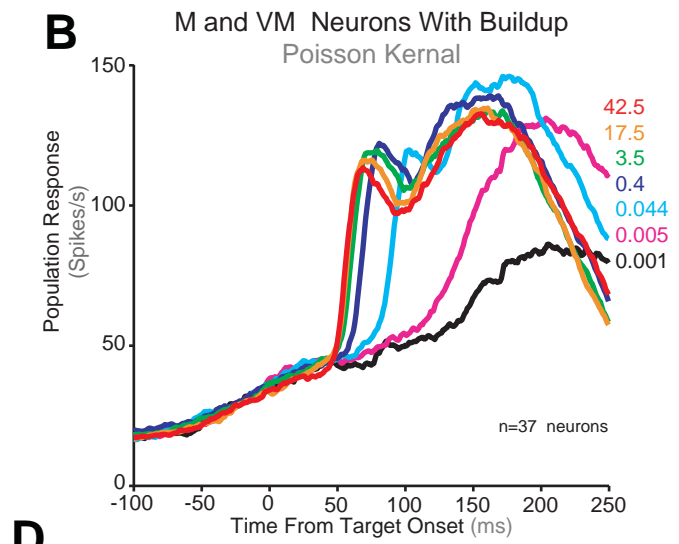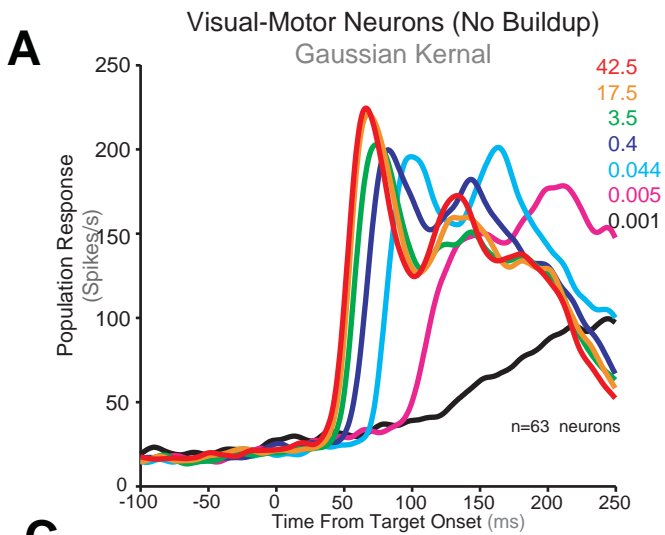Marino et al. Fig. 4

Express Vs Regular Saccades (VM Neurons)

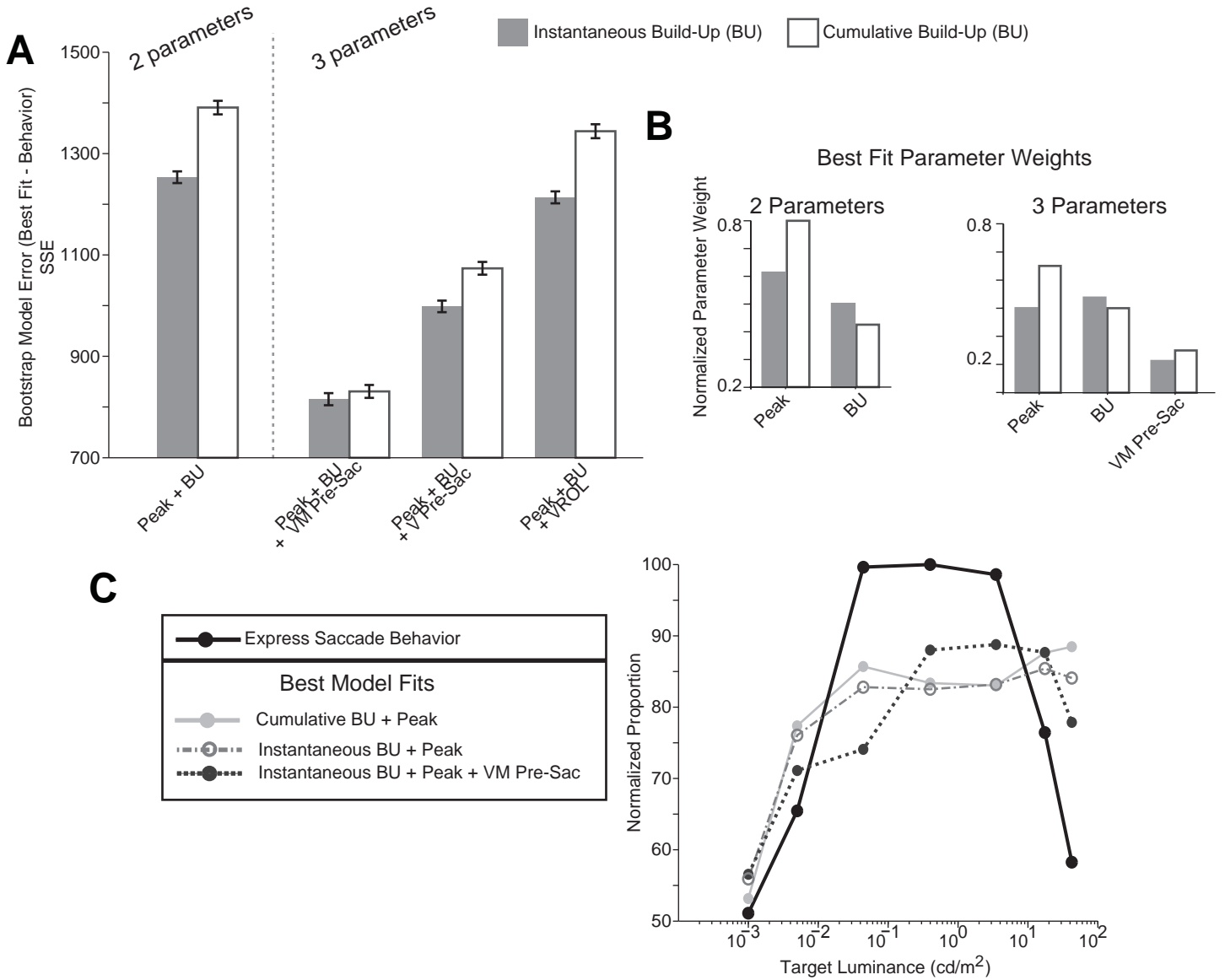**A**

0.001 cd/m²
Express (dotted)
Regular (solid)

0.005 cd/m²

0.044 cd/m²

0.4 cd/m²

3.5 cd/m²

17.5 cd/m²

42.5 cd/m²

Activity (Spikes/s)

Time from Target Appearance (ms)

B

0.001 cd/m²   n=48

0.005 cd/m²   n=58

0.044 cd/m²   n=59

0.4 cd/m²   n=52

3.5 cd/m²   n=55

17.5 cd/m²   n=41

42.5 cd/m²   n=33

Time from Saccade Start (ms)

Marino et al. Fig. 5

Marino et al. Fig. 6

Marino et al. Fig. 7

Marino et al. Fig. 8