

Saccade suppression depends on context

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Abstract

Although our eyes are in constant movement, we remain unaware of the high-speed stimulation produced by the retinal displacement. Vision is drastically reduced at the time of saccades. Here, I investigated whether the reduction of the unwanted disturbance could be established through a saccade-contingent habituation to intra-saccadic displacements. In more than 100 context trials, participants were exposed either to an intra-saccadic or to a post-saccadic disturbance or to no disturbance at all. After induction of a specific context, I measured peri-saccadic suppression. Displacement discrimination thresholds of observers were high after participants were exposed to an intra-saccadic disturbance. However, after exposure to a post-saccadic disturbance or a context without any intra-saccadic stimulation, displacement discrimination improved such that observers were able to see shifts as during fixation. Saccade-contingent habituation might explain why we do not perceive trans-saccadic retinal stimulation during saccades.

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34 **Introduction**

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36 The sensorimotor contingency theory proclaims that perception consists in mastering the
37 systematic relations between actions and their perceptual consequences (O'Regan and
38 Noe, 2001). The prime example for sensorimotor contingencies are those movements we
39 perform most often in real life, i.e. saccade eye movements and the associated motion
40 stimulation they produce. Every time we perform a saccade the external world sweeps with
41 high speed motion across the retina. Consequently, the visual system has to deal with two
42 challenges: First, to keep in register where in external space each pre- and post-saccadic
43 image originated from, and second, to suppress any motion sensation that would arise
44 during the retinal displacement.

45 Learning sensorimotor contingencies requires a signal that indicates the initiation of a
46 movement. In eye movement research, the concept of the efference copy arose, that is a
47 signal which informs visual areas about the metrics of upcoming eye movements (Wurtz,
48 2008). To guarantee the spatial alignment across saccades between internal and external
49 space, neurons in the intra-parietal cortex (Duhamel et al., 1992), in the frontal eye fields
50 (Umeno & Goldberg, 1997), the superior colliculus (Walker, Fitzgibbon, & Goldberg, 1995)
51 and in visual areas V2 and V3 (Nakamura & Colby, 2002) shift their receptive fields
52 predictively, triggered by an efference copy signal (Sommer and Wurtz, 2006). The
53 suppression of intra-saccadic motion perception might be driven by such an extra-retinal
54 signal likewise (for a review, see Binda and Morrone, 2018).

55 As it has been shown that the visual system is able to detect high-speed motion (Burr et
56 al., 1982) the question arises why we are not aware of the motion stimulation produced by
57 a saccade. In the search for a mechanism that cancels trans-saccadic motion perception,
58 researchers have found that sensitivity of visual contrast (Volkman et al.1978) and of
59 motion (Burr et al., 1982; Shioiri & Cavanagh 1989; Ilg and Hoffman, 1993) drops down at
60 the time of saccades. This process - called saccade omission - amounts to 0.5-1 log units,
61 is strongest for low spatial frequencies (Volkman, 1986; Burr et al., 1994) and is
62 homogeneous across the visual field (Knöll et al., 2011). It starts ~50 ms before saccade
63 initiation, peaks around saccade onset and fades away 50 ms later (Volkman et al.1978).
64 It has been argued that the intra-saccadic decrease of visual sensitivity is the signature of

a mechanism that shuts down the magnocellular pathway at an early neural level to prevent the disturbing motion experience during saccades (Burr et al. 1994). However, in contrast to an early shut-down resulting in motion blindness, Castet and Masson, (2000) have demonstrated that motion detection during saccades is still possible if stimuli are optimized for high-speed motion detection. They used low-contrast gratings drifting at a constant high speed (360 dva/s) and found that the ability to perceive intra-saccadic motion depended on the difference between the peak eye velocity and grating speed. In their view, the magnocellular pathway is still active at the time of saccades and the peri-saccadic reduction of contrast sensitivity results from retinal factors (Castet, Jeanjean & Masson, 2002). In a follow-up study the same authors could further show that this ability to perceive fast intra-saccadic motion declined when additional pre - and post-saccadic stimuli were visible. They suggested that these static images masked intra-saccadic motion thus reducing awareness. Indeed, masking has been shown to also cancel out the retinal smear produced by the saccade (Campbell & Wurtz, 1978). Duyck, Collins & Wexler (2016) recently devised a method to test the perception of intra-saccadic smear objectively and thereby corroborated the idea that masking hides saccade-induced motion from perception. In that study smear-masking survived a dichoptic presentation thus suggesting a central origin. If masking and not saccade-related mechanisms explains saccadic omission, one should find masking-induced suppression even in the absence of saccades. Recently, Duyck, Wexler, Castet and Collins (2018) used simulated saccades and found motion perception to be much less salient in the presence of static objects. While masking provides a very parsimonious account of how the retinal smear remains hidden from awareness, it is still an open question why we do not consciously perceive a motion transient from the pre-saccadic to the post saccadic image. It is long known that trans-saccadic displacements of a certain size go unnoticed by the observer (Bridgeman, Hendry, & Stark, 1975; Niemeier, Crawford, & Tweed, 2003), a phenomenon termed saccadic suppression of displacement. The reason for the poor displacement detection is that the saccade covers the motion transient because the presence of motion transients leads to very high displacement sensitivity (Legge & Campbell, 1981). Here, I offer a novel explanation of suppression which states that the brain stores and habituates to sensorimotor contingencies. This account does not require elimination of peri-saccadic perception via contrast reduction at an early processing level. I show that the

98 saccadic suppression results from a habituation to intra-saccadic stimulation (see Figure
99 1). In this view, neurons in an extra-retinal storage mechanism will be informed by an
100 efference copy about the initiation of a saccade, store saccade-induced visual stimulation
101 and saturate their response to the visual information most dominant in the previous history
102 of the last set of saccades that has been executed.

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104 This idea predicts that suppression magnitude can be modulated by the visual context in
105 which saccades are performed. Performing saccades in a structured environment induces
106 recurring intra-saccadic stimulation. In order to create an experimental environment in
107 which intra-saccadic information could be systematically varied, I used a horizontal grating
108 as a background on which horizontal saccades had to be performed. As the grating was
109 oriented parallel to the saccade path it should have produced only negligible retinal motion
110 information. Context-sensitivity would predict that performing many saccades on that
111 background should lead to a minimal magnitude of saccade suppression compared to
112 natural vision, where saccades are performed mostly across structured environments.

113

114 The intra-saccadic stimulation was displayed as soon as a saccade was detected. I used a
115 grating displacement orthogonal to the rightward saccades, i.e. upward displacements of
116 the horizontal grating, in order to disentangle the artificially produced shift (the grating
117 displacement) from the retinal motion. Testing displacement discrimination parallel to the
118 saccade path requires more sophisticated experimental designs (Castet and Masson,
119 2000) that would have led to an unjustifiable number of trials. If the sensorimotor system
120 takes into account this exposure, intra-saccadic displacement detection should drastically
121 decline. Consistent with context-sensitivity, saccade suppression magnitude was strong
122 when observers performed many trials in which stimulation was presented contingent on
123 saccade execution. However, saccade suppression was absent if the background grating
124 remained stationary and observers were able to perceive intra-saccadic motion as well as
125 during fixation.

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Results

I asked participants to perform horizontal, rightward saccades in a dark environment. Stimuli were presented on a computer screen that was covered by a semi-transparent foil in order to dampen visual stimulation as much as possible. The background consisted of a sinusoidal horizontal grating shown with a spatial frequency of 0.05 c/dva (see Figure 2A). At the start of each experimental session (except baseline), participants performed 105 saccades over the grating. In these context trials - depending on the session - the grating was displaced either during or after the saccade or it remained stationary.

Shifting the grating during saccade execution allowed to systematically manipulate intra-saccadic stimulation. Figure 2B shows the time-course of events for sessions in which the grating was shifted upward as soon as the eye-tracker detected saccade initiation. After a fixation period of 1000-1500 ms the saccade target was presented only briefly and participants started their saccades after the disappearance of the fixation point. Since the experiment was conducted in a dark room and the monitor screen was covered by a semitransparent foil, no visual information except the shifting grating was present during saccade execution. I checked the timing of the grating displacement relative to saccade performance in an offline analysis. Depending on sessions, displacements were presented well within (see Figure 2C) or outside (see Figure 2D) the period of saccade execution,. Figure 2E summarizes all five conditions tested in the experiment. Baseline sessions contained no context but only test trials. The remaining four sessions that did contain context trials, comprised a condition with no grating displacement and conditions with a displacement of the grating 37.89 ms (SEM 5.94 ms), 98.07 ms (SEM 8.59 ms) or 186.99 ms (SEM 7.92 ms) after saccade initiation.

After the presentation of the context trials, I tested displacement discrimination in a 2-alternative forced-choice task for a grating that was shifted either upwards or downwards (Figure 2F). The time-course of events was identical to that of the context trials except that

164 the shift of the grating was applied at various times around saccade execution. I analyzed
165 displacement discrimination performance relative to saccade onset in bins of 30 ms.
166 Figure 2G shows displacement discrimination results of all participants from sessions in
167 which the grating was shifted upward 35 ms after saccade onset in the context trials. Data
168 were taken from a bin long before saccade initiation (< -50 ms to saccade onset, shown in
169 gray) and from a bin close to saccade onset (-25 ms $<$ saccade onset < 25 ms, shown in
170 purple). Data were fitted by cumulative gaussian functions and performance determined by
171 estimating the JND of the psychometric function.

172
173 Psychometric functions for grating displacements presented during the saccade are far
174 shallower indicating higher thresholds or stronger suppression. Thus, suppression
175 magnitude was strong when in the context trials the grating shifted upwards during
176 saccade performance. Data shown in Figure 2H derive from sessions in which the grating
177 was not displaced in the context trials. For all observers, JNDs of the psychometric
178 functions from intra-saccadic bins were steeper than those measured after context trials in
179 which the grating was displaced.

180
181 Figure 3A shows the full time course of displacement thresholds around the time of
182 saccade execution for all observers. Data derive from sessions in which the grating was
183 shifted 35 ms after saccade initiation. For all observers, intra-saccadic discrimination
184 performance declined after they had performed saccades with intra-saccadic stimulation in
185 the context trials. Figure 3B shows displacement thresholds from sessions where the
186 grating was not shifted in the context trials. In order to quantify intra-saccade displacement
187 discrimination, ie. suppression magnitude, I chose the peak thresholds that were contained
188 in a bin ± 50 ms around saccade initiation. For the quantification of displacement
189 discrimination during fixation, I calculated the average over all bins lying at least 100 ms
190 before and 100 ms after saccade onset.

191
192 I analyzed saccade parameters in order to estimate a putative influence of saccade
193 amplitudes on suppression strength (Volkman et al., 1981; Stevenson et al., 1986) in my
194 data. Figure 3D,E shows horizontal and vertical average saccade amplitudes for all five
195 sessions. In all sessions, saccades show the typical undershoot of the required amplitude
196 (20°). Similarly, no statistical differences were found between average peak velocities of

saccades (see Figure 3C). It has been shown that background displacement can provoke saccade adaptation (Deubel, 1991; Robinson et al., 2000; Ditterich et al., 2000).

The recurring upward displacement of the background might have induced adaptation of the vertical saccade component. I subtracted the last ten vertical saccade amplitudes of the context trials by the first ten to check for an adaptation of saccadic gain. Figure 3F shows saccade gain change for all four sessions that contained context trials. I calculated one-tailed paired t-tests separately for all four sessions. There was no statistical evidence for a significant gain change in any of the sessions (context 35 ms: $t(3) = 1.18$, $p = 0.32$, context 98 ms: $t(3) = -0.60$, $p = 0.59$, context 187 ms: $t(3) = -0.66$, $p = 0.55$, context no motion: $t(3) = 0.21$, $p = 0.85$).

Figure 3G shows displacement discrimination averaged across all 4 participants from the peri-saccade period (shown in red) and the fixation period (shown in gray) in baseline sessions where no context trials were applied. Observers demonstrated poor peri-saccadic displacement discrimination as is expected if suppression is not absent. Gratings had to be shifted upwards on average ~ 120 deg (phase shift) such that observers were able to tell the correct direction of the shift. A paired one-tailed T-test confirmed that displacement discrimination thresholds were significantly higher when the grating was shifted peri-saccadically than before saccade initiation ($t(3) = -9.38$, $p = 0.0026$). The effect size of this difference was 1.7 (Cohen's d) which is considered a very large effect. Figure 3H shows average displacement discrimination from sessions that included context trials. Intra-saccadic displacement discrimination thresholds were virtually identical to those of the baseline sessions if in the preceding context trials the grating was displaced during saccade execution, i.e. 35 ms after saccade onset. However, thresholds decreased massively after participants performed context trials in which the displacement occurred after the saccade had landed or in which there was no displacement at all. In these sessions, peri-saccade displacement discrimination was almost as good as during fixation. This finding provides clear evidence for the idea that the sensorimotor system habituates to peri-saccadic stimulation. In sessions where the grating was shifted outside the period of saccade execution, the system was relieved of suppression since no intra-saccadic stimulation occurred for more than 100 trials. For statistical analysis, I calculated the difference between baseline and adaptation sessions within each participant and averaged across all post-saccadic / no motion difference values (i.e. the 96, 187 ms and the No

230 motion context data) within each participant. A paired one-tailed T-test confirmed that
231 intra-saccadic stimulation in the context trials induces stronger suppression than post-
232 saccadic / no displacement stimulation ($t(3) = 3.68$, $p = 0.017$).

233 In order to better understand the effect of the intra-saccadic stimulation, I analyzed the
234 biases of the displacement discrimination. Figure 3I shows biases for fixation (gray) and
235 peri-saccade discrimination from the baseline sessions. A paired one-tailed T-test did not
236 reveal a significant differences ($t(3) = -1.63$, $p = 0.20$). Similarly in the discrimination data
237 that followed context trials, no significant difference in biases between conditions was
238 found (see Figure 3J). Thus, there was no evidence for a motion after-effect in the current
239 data that would have manifested in changed bias, i.e. a shift of the psychometric functions.
240 Next, I sought to find out whether the habituation effect is direction-specific. To this end, I
241 modified the display of the test trials to contain two horizontal gratings (see Figure 4A).
242 The experiment contained context and test trials. In the test trials, participants were
243 required to perform a saccade to the remembered position of the saccade target as in the
244 first experiment. Then, they had to judge which of the two gratings was displaced. The
245 displacement direction in the test trials was always upwards and applied either during
246 saccade or after saccade execution. The displacement direction in the context trials was,
247 in separate sessions, either upwards or downwards with the same displacement size of 57
248 deg phase shift as in the other experiments. A clear elevation of discrimination thresholds
249 was observed only if the displacement in the context trials occurred during the saccade
250 and had the same direction (upwards) as in the test trials (see Figure 4B). A non-
251 parametric repeated measures ANOVA with the factors “displacement direction” (upward /
252 downward) and “displacement time” (during / after saccade) revealed a significant main
253 effect “displacement direction” ($F(1,4)=15.65$, $p=0.017$), confirming that thresholds were
254 elevated selectively when the displacement direction in the context and the test trials
255 matched. The significant interaction effect ($F(1,4)=8.18$, $p=0.046$) revealed that the
256 selectivity was observed only when the displacement occurred during but not after
257 saccade execution. The factor “displacement time” was not significant ($F(1,4)=6.668$,
258 $p=0.061$).

259 Displacing a stimulus during execution of a saccade produces a different retinal motion
260 vector as a displacement during ocular fixation. The retinal motion vector is the sum of the
261 physical displacement vector (i.e. upward) and the inverse saccade vector (i.e. leftward for
262 rightward saccades). Even though the screen borders were covered by a foil and the room

263 was dark, the vertical edges of the horizontal grating might have contributed to the
264 experience of a horizontal motion component. In order to compare habituation for intra-
265 saccadic and post-saccadic presentations with a matched retinal motion vector, I
266 conducted a new experiment. In this Experiment 3, I added vertical bars to the horizontal
267 grating to imitate leftward motion of the vertical grating edges. The spatial frequency of the
268 vertical bars and the horizontal grating was kept identical. The procedure was identical to
269 Experiment 2 except that only in the test trials the displacement now contained a
270 horizontal component in addition to the vertical. The amount of the horizontal component
271 was calculated to be identical to the saccade-induced horizontal shift of the grating
272 displacement measured in Experiment 2 (see Methods section for details). I tested
273 sessions with an upward displacement in the context trials (see Figure 5B) and a
274 downward displacement (see Figure 5C). In the test trials the physical displacement was
275 either upward or downward when presented in the intra-saccadic period or it was upward +
276 leftward or downward + leftward when presented in the post-saccadic period. As in
277 Experiment 2, habituation was much stronger in the intra-saccadic period and selective for
278 the direction of the displacement.

279 A non-parametric repeated measures ANOVA was calculated separately for data deriving
280 from sessions with upward displacements in the context trials (see Figure 5B) and from
281 those including downward displacements (see Figure 5C). For contexts with upward
282 displacements, a significant main effect “displacement time” ($F(1,4)=65.556$, $p < 0.001$)
283 and a significant interaction effect ($F(1,4)=19.883$, $p=0.011$) was revealed, confirming that
284 the selective decrease of discrimination occurred during but not after saccade
285 performance. The factor “displacement direction” was not significant ($F(1,4)=5.00$, $p =$
286 0.089). For contexts with downward displacements, a significant main effect “displacement
287 time” ($F(1,4)=16.337$, $p=0.016$) and a significant interaction effect ($F(1,4)=25.600$,
288 $p=0.007$) was revealed, confirming that the selective decrease of discrimination occurred
289 during but not after saccade performance. The factor “displacement direction” was not
290 significant ($F(1,4)=4.986$, $p=0.089$).

291

292 **Discussion**

293 The results of this study clearly demonstrate that saccade suppression magnitude is
294 strongly modulated by the recent context of intra-saccadic stimulation. After hundreds of

295 saccades without intra-saccadic stimulation, observers were able to detect intra-saccadic
296 displacements almost as good as during fixation. However, if the displacement was
297 presented systematically within the period of saccade execution, thresholds increased
298 drastically. The visual system habituates context-dependent to saccade-contingent visual
299 information. This results provides evidence for a possible mechanism of peri-saccadic
300 suppression. Instead of a general shut-down of vision, neurons might saturate to the
301 information most prevalent in the previous saccadic context and thereby cancel out
302 disturbing intra-saccadic stimulation. Importantly, any visual adaptation induced was
303 contingent on the execution of a saccade. No habituation effect was found when the
304 stimulation in the context trials was presented after a saccade had finished. The context
305 dependent habituation therefore requires an extra-retinal signal that informs visual areas
306 about the upcoming saccade. Such a context-dependence would be consistent with a
307 recent Kalman filter model of saccade suppression in which higher variance in sensory
308 feedback yields a reduced sensory weight, thereby decreasing sensitivity (Crevecoeur &
309 Körding, 2017). In the model, the strength of saccade suppression is dynamically linked to
310 the predicted reliability of the intra-saccadic sensory signal.

311 However, from the present data it cannot be determined how stimulus-specific trans-
312 saccadic habituation is. Although I found direction-selectivity, it cannot be ruled out that
313 habituation would also occur for changes of form or any visual stimulus occurring
314 transiently during the saccade. One plausible candidate for the habituation to trans-
315 saccadic displacements might be saturation of motion-sensitive neurons. Saturation of
316 neuronal responses after short-term motion adaptation has been reported to occur in area
317 MT (Priebe et al., 2002). The idea of the extra-retinal storage (see Figure 1) does not
318 exclude however, that habituation occurs for any stimulus feature that reoccurs during
319 saccade performance. This question should be pursued in future research by testing
320 whether habituation is selective for trans-saccadic motion stimuli or if it generalizes across
321 other visual features. The experimental task that I applied can in principle be solved
322 without relying on motion information. The direction of a displacement can be detected by
323 two ways: By noticing the motion transient between the first and the second image or if
324 that is not possible by comparing feature locations of the first and the second image.
325 Displacement detection is strong during ocular fixation (Legge & Campbell, 1981) but
326 weak during saccades (Bridgeman, Hendry, & Stark, 1975; Deubel & Schneider, 1996;
327 Niemeier, Crawford, & Tweed, 2003)). In order to compare the results of the current study

328 to the phenomenon of suppression of displacement, one should look at studies that
329 displaced the saccade target constantly in the same direction before testing displacement
330 detection. This was done when the effect of saccade adaptation on displacement detection
331 was tested (Collins et al., 2009). In this study, no effect of saccade adaptation trials on the
332 displacement thresholds was observed (see their Figure 3C). However what they did
333 report was a shift of the bias in displacement detection after saccade adaptation. In my
334 study however, the bias of displacement discrimination was statistically indistinguishable
335 before and after the context trials. In the absence of a conscious displacement detection,
336 the oculomotor system might be aware of the shift and - in the case of systematic
337 displacements - adapt to it. Some studies have shown that saccades not only adapt to
338 intra-saccadic jumps of the saccade target but also to displacements of the background
339 (Deubel, 1991; Robinson et al., 2000; Ditterich et al., 2000). I compared the first and the
340 last 10 saccade amplitudes of the context trials and did not find significant changes that
341 would indicate adaptation. The most likely reason for the absence of adaptation is that the
342 previous studies used background images containing focal elements that allow estimating
343 the distance to the eye position. An increase of visual sensitivity starting around 50 ms
344 before saccade onset can be observed at the focus of attention, i.e. the saccade target
345 (Rolfs & Carrasco, 2012). However, I used a low-frequency sinusoidal grating without clear
346 edge information. In the experiments of the present study, it cannot be decided to what
347 extent participants employed a comparison between the pre-and post-saccadic image and
348 how much they used the motion transient to judge the displacement. In real life we
349 constantly perform saccades of various sizes and directions, producing different retinal
350 motion stimulations. The direction-selectivity that I found suggests that different saccade
351 vectors are connected to habituation of different displacement directions. If there would a
352 general insensitivity to displacements, direction-selectivity could not have been observed.

353 It has been suggested that suppression of trans-saccadic displacements is determined by
354 peri-saccadic suppression of contrast sensitivity. In this view, an active mechanism
355 transiently shuts down the magnocellular pathway and thereby prevents an intra-saccadic
356 motion sensation (Burr et al., 1994). Others have demonstrated that some intra-saccadic
357 motion perception is possible if stimuli are made optimal to compensate for the retinal
358 displacement (Castet and Masson, 2000). Testing whether suppression of visual sensitivity
359 is context-sensitive as well could answer the question of a link between peri-saccadic
360 contrast sensitivity and displacement discrimination directly. Under the assumption of such

361 a linkage, performing a number of saccades on a background with high contrast (even
362 without motion information) should increase peri-saccadic displacement thresholds.
363 However, the direction selectivity that I found indicates already that the habituation cannot
364 be explained by the decrease in contrast sensitivity which would affect all displacement
365 directions likewise.
366 Peri-saccadic increase in contrast thresholds might underlie a similar habituation
367 mechanism. It has been repeatedly reported that contrast suppression (Brooks and Fuchs,
368 1975; Brooks et al., 1980a; Mitrani et al., 1971; Richards, 1969) and the neural
369 modulations in area MT (Price et al., 2005) are absent when tested under dark conditions.
370 Consistently, intra-saccadic motion becomes visible if the light is switched on only during
371 execution of the saccade (Campbell and Wurtz, 1978). However, suppression remains
372 strong when saccades are made under ocular diffuser or in a Ganzfeld (Riggs et al.,
373 1982). Since the peri-saccadic stimulation is identical in the dark and the Ganzfeld and
374 only the illumination differs, the differences between suppression under both conditions
375 cannot be attributed to backward masking. The visual system can habituate to intra-
376 saccadic motion only under light conditions, thus probably explaining the absence of
377 suppression in the dark. If suppression of visual contrast depends on context, performing a
378 number of saccades in the Ganzfeld should release habituation and thereby increase intra-
379 saccadic contrast sensitivity.

380

381 In conclusion, the data of the present study indicate that saccade suppression is context
382 dependent. The experiments suggest a simple mechanism that explains how the
383 disturbing intra-saccadic experience is prohibited by saccade-contingent neuronal
384 habituation.

385

386

387 **Methods**

388

389 **Apparatus**

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391 Subjects were seated 45 cm from a Eizo FlexScan T57S with the head stabilized by a
392 forehead rest. The visible screen diagonal was 20 in., resulting in a visual field of 40 diva ×

393 30 dva. Stimuli were presented on the monitor with a vertical frequency of 120 Hz on a
394 homogeneous gray background.

395 Participants

396 Four subjects participated in the context-selectivity experiment (2 female, 2 male, mean
397 age: 28; 3 naive to the purpose of each condition and the author), five subjects in
398 Experiment 2 (3 female, 2 male, mean age: 29; 4 different subjects than in Experiment 1
399 and naive to the purpose of each condition and the author) and five subjects in Experiment
400 3 (4 female, 1 male, mean age: 29; 3 different subjects than in Experiment 1 and naive to
401 the purpose of each condition, one subject that already participated in Experiment 2 and
402 the author). All subjects had normal or corrected-to-normal vision. Experimental
403 procedures were approved the local ethics committee of the psychological department of
404 the Heinrich- Heine University Düsseldorf. Written informed consent was obtained prior to
405 each experiment in accordance with the declaration of Helsinki.

406

407 Eye movement recording

408 Eye movements were monitored by the EyeLink 1000 system (SR Research), which
409 samples gaze positions with a frequency of 1000 Hz. Viewing was binocular, but only the
410 dominant eye was recorded. A standard 9 point calibration was performed at the beginning
411 of each block of trials. The system detected the start and the end of a saccade when eye
412 velocity exceeded or fell below 22 dva/s and acceleration was above or below 4000 dva/s²
413 respectively.

414

415 Timing of stimulus presentation

416 In order to test the exact time of stimulus presentation on the screen, I used a photodiode
417 that was connected to an electronic circuit and sent a TTL impulse to the parallel port of
418 the eyelink PC for every luminance change on the screen. A lowpass filter prohibited that
419 the luminance change at the time of the screen refresh entered into signal recording. This
420 measuring device was custom built with electronic parts. The delay of the device itself was
421 measured by an oscilloscope and found to operate in the nanosecond range. Thus, the
422 measuring device plus the recording in the eyelink PC should not have added any

detectable delay. In the analysis, I compared the timestamp of the message that my stimulus program sent to the Eyelink PC against the timestamp of the TTL impulse sent by the measuring device. With the setup that I used this display lag was measured to be on average 4.35 ms (S.E.M. 0.29). Therefore, I added 4.35 ms to all data in the analysis.

Trial structure and data analysis

In all experiments, a session contained 385 trials. Experiment 1 consisted of 5 different types of session. Four of these sessions each contained context trials in which motion was displayed relative to the saccade (grating moved 35 / 98 / 187 ms after saccade onset) or no was displayed (grating remained stationary). Importantly, in one session only one type of context trials was presented. The fifth type of sessions were baseline sessions which did not contain context trials. In order to obtain sufficient data for the estimation of the suppression curve, participants repeated sessions of each context type several times (context 35 ms: 8 (S.E. 1.96), context 98 ms: 6 (S.E. 1.22), context 187 ms: 6.5 (S.E. 0.96), context no motion: 4 (S.E. 0.91) , baseline: 7.75 (S.E. 0.75)). The order in which participants completed these sessions was randomized. The required saccade distance in each trial of all experiments was 20 dva. Trials in which saccade amplitudes were shorter than 10 dva were excluded from analysis.

For statistical analysis of Experiments 2 and 3, a non-parametric repeated measures ANOVA was calculated, using the Aligned Rank Transform (Wobbrock et al., 2011). Significance was determined by applying the Kenward-Roger approximation to estimate p-values, a procedure that has been shown to produce acceptable Type 1 error rates even for smaller samples (Luke, 2017).

Procedure

All experiments were carried out in a complete dark environment. To avoid visibility of the screen borders, the display was covered with a transparent foil that reduced the luminance by about 2 log units. Each experimental session, except baseline sessions, contained context trials and test trials (see Figure 1E). Context sessions began with 105 context trials. After these, 5 test trials alternated with 5 context trials until the end of the session,

456 containing 385 trials in total.

457 In Experiment 1, a context trial started with the presentation of a horizontal sinusoidal
458 grating (spatial frequency: 0.05 c/dva, Michelson-contrast: 0.56, mean luminance: 0.15
459 cd/m^2) that was displayed full-screen (see Figure 1A). On top of the grating a fixation
460 rectangle (green, 0.75 dva x 0.75 dva) was shown 10 dva to the left of screen centre at the
461 horizontal meridian. After a randomly chosen period between 1000 - 1500 ms, a saccade
462 target (green, 0.75 dva x 0.75 dva) was shown while the fixation rectangle remained
463 visible. After 60 ms, both, fixation rectangle and saccade target disappeared and
464 participants performed a rightward saccade to the remembered position of the target. In all
465 sessions rightward saccades were tested. The detection of the saccade by the eye-tracker
466 triggered the displacement of the grating. Three different grating displacement times were
467 programmed that were applied in separate sessions: The physical displacement occurred
468 on average either 34.89 ms (SEM 5.94 ms) with a saccade duration of 58.67 ms (SEM
469 4.86 ms), 98.07 ms (SEM 8.59 ms) with a saccade duration of 52.32 ms (SEM 7.94 ms) or
470 186.99 ms (SEM 7.92 ms) with a saccade duration of 64.12 ms (SEM 6.23 ms) after
471 saccade initiation. The grating displacement size in context trials was always 57 deg
472 phase shift for one frame in upward direction. When participants had finished their
473 saccade, they pressed one of the arrow keys to start the next trial. Test trials were
474 identical to context trials except that the fixation point turned red and the intra-saccadic
475 displacement of the grating could be upwards or downwards with one out of 7 possible
476 displacement sizes (-115 deg, -76 deg, -38 deg, 0 deg, 38 deg, 76 deg, 115 deg phase
477 shift). Each displacement size was presented 10 times in pseudo-randomized order.
478 Participants were instructed to discriminate between upward and downward displacements
479 by pressing the corresponding arrow key. After they pressed the response button a new
480 trial started and participants re-directed their gaze to the fixation rectangle. During the
481 leftward saccade to the fixation rectangle the grating remained stationary. Baseline
482 sessions contained only test trials. From these data psychometric functions were
483 determined by fitting cumulative gaussian functions to the motion discrimination data from
484 each observer.

485 In Experiment 2, I measured the direction-selectivity of contextual habituation. All sessions
486 in these experiments contained context and test trials. In context trials a full-screen grating
487 (spatial frequency: 0.2 c/dva, Michelson-contrast: 0.56, mean luminance: 0.15 cd/m^2) was
488 presented that was - depending on session - displaced either during (i.e. 35 ms after

saccade onset) or after (i.e. 98 ms after saccade onset) saccade execution. Each session contained 100 context trials after which 5 test trials alternated with 5 context trials. In test trials two gratings (each: spatial frequency: 0.2 c/dva, Michelson-contrast: 0.56, mean luminance: 0.15 cd/m²) were shown, one on each side of the screen (see Figure 3A). At trial start, a fixation point was shown for 1000-1500 ms. Then, a saccade target appeared for 60 ms after which both, the fixation point and the saccade target disappeared. The participants were instructed to perform a saccade to the remembered position of the saccade target as soon as it had disappeared. In test trials, one of the two gratings was displaced as soon as the eye-tracker detected saccade onset. The physical displacement occurred - depending on session - on average either 32.53 ms (SEM 0.94 ms) with a saccade duration of 52.8 ms (SEM 3.45 ms) after saccade initiation or 97.22 ms (SEM 0.78 ms) after saccade initiation with a saccade duration of 50.85 ms (SEM 4.66 ms). The displacement was chosen randomly across trials out of 7 possible sizes (-115 deg, -76 deg, -38 deg, 0 deg, 38 deg, 76 deg, 115 deg phase shift). Participants were instructed to indicate which of the two gratings was moved by pressing either the left or right arrow key.

A direct comparison of contextual habituation between intra-saccadic and post-saccadic motion discrimination is hindered by the fact that in intra-saccadic test trials the displacement is shifted on the retina by the saccade whereas in post-saccadic trials it is not. In Experiment 3, I tested the direction-selectivity of contextual habituation by matching the retinal motion vector imposed in intra-saccadic displacements with the motion vector in post-saccadic displacements. In Experiment 1 and 2 the physical displacement was vertical. For intra-saccadic displacements, the motion vector is the sum of the physical displacement direction and the direction of the retinal movement itself (i.e. leftward motion for a rightward saccade).

Experiment 3 was identical to Experiment 2, except that the grating displacement direction in the test trials was different. In order to present an oblique motion vector in the test trials, I now used a grating that contained vertical and horizontal bars (see Figure 4). The physical displacement occurred - depending on session - on average either 34.58 ms (SEM 0.78 ms) with a saccade duration of 67.8 ms (SEM 4.42 ms) after saccade initiation or 94.07 ms (SEM 4.06 ms) after saccade initiation with a saccade duration of 68.95 ms (SEM 3.56 ms). As the aim of Experiment 3 was to imitate the displacement of the horizontal grating edge produced by the saccade, one single bar could have been presented. However, one single bar would have served as an ideal landmark for

522 localization. To prevent the use of such a landmark, I used the same spatial frequency for
523 the generation of the vertical and the horizontal bars (0.2 c/dva). These vertical bars were
524 generated by a sinusoidal function (each: spatial frequency: 0.2 c/dva, Michelson-contrast:
525 0.56, mean luminance: 0.15 cd/m²) but only a quarter of a cycle around the peak of the
526 minimum luminance was shown (i.e. the dark bar). To estimate the displacement size that
527 would mimic the retinal shift produced by the saccades, I used the average data of
528 Experiment 2 and calculated the average eye velocity at the time of the displacements. To
529 this end, I selected eye position samples that were recorded within 8 ms (i.e. one frame)
530 after the time of the physical grating displacement. With these samples, I calculated the
531 eye velocity at the frame that the displacement occurred ($v_{eye} = 181.25$ dva/s). Then, I
532 computed the necessary temporal frequency (f_T) of the grating that would mimic the eye
533 velocity at the given frame rate (fps = 120 Hz) and the given spatial frequency of the
534 grating ($f_S = 0.2$ c/dva) by solving the equation: $f_T / f_S = v_{eye}$ (36.25 c/s / 0.2 c/dva = 181.25
535 dva/s), dividing by the frame rate (36.25 c/s / $120 = 0.302$ c/fps), i.e
536 $0.302 \times 2 \times \pi = 1.89$ radians or 108.29 degrees.

537

538

539 **Ethics**

540 The study was approved by the ethics committee of the Faculty of Mathematics and
541 Natural Sciences of the Heinrich-Heine-University Duesseldorf (ZI01-2019-01) and in
542 accordance with the declaration of Helsinki.

543

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674 Nonparametric Factorial Analyses Using Only ANOVA Procedures.” In Proceedings of the
675 ACM Conference on Human Factors in Computing Systems (CHI '11), 143–146.

676

677

678

679 Captions

680 Figure 1

681 **A** Schematic illustration of the proposed model. For saccade generation, a motor
682 command is sent to the motor plant which produces the desired eye movement. Intra-
683 saccadic visual stimulation will activate an extra-retinal storage mechanism. Importantly,
684 this storage mechanism is activated only under the combined condition that an efferent
685 copy signals the occurrence of an eye movement and visual stimulation is sensed.
686 **B** Recurring input of visual stimulation will habituate neurons in the extra-retinal storage,
687 consequently leading to a reduced sensitivity for intra-saccadic stimulation. In a context
688 with low retinal stimulation, habituation remains weak and intra-saccadic neuronal
689 responses to visual stimulation remain comparable to fixation. However, in a context with
690 high retinal stimulation neurons habituate and intra-saccadic neuronal responses become
691 weak.

692

693 Figure 2

694 **A** Schematic illustration of a context trial. A full-field grating was presented throughout the
695 entire trial. A trial started with the presentation of a fixation point. After 1000-1500 ms a
696 saccade target was presented together with the fixation point for 60 ms. Then, both, the
697 saccade target and the fixation point disappeared. Subjects were instructed to perform a
698 saccade to the remembered position of the saccade target as soon as the fixation point
699 disappeared. Depending on the session, the grating was displaced upwards after 35, 98,
700 187 ms or not displaced at all.
701 **B** Time-course of events in the context trials for the fixation point (FP), the saccade target
702 (ST), the 7 horizontal eye position (H EP) and the grating displacement (Motion).
703 **C,D** Example eye velocity profiles from one participant representing saccade performance
704 in the context trials (shown in blue). Average eye position is shown by the blue line.

705 Average timing of the actual grating displacement is shown by the red vertical line and the
706 standard deviation of the timing by the shaded area.

707 **E** Summary of conditions. Baseline sessions consisted only of test trials. The remaining
708 four sessions contained context and test trials. In these sessions the grating was displaced
709 35, 98, 187 ms after saccade execution or not displaced at all.

710 **F** Schematic illustration of a displacement discrimination trial. These trials were identical to
711 the context trials except that the grating was shifted upwards or downwards (indicated by
712 the orange arrows) by various displacement sizes and across trials at various times
713 relative to saccade onset. Participants were instructed to report the displacement direction
714 at the end of the trial by pressing the corresponding arrow key on the computer keyboard.

715 **G,H** Psychometric functions for judgements of the displacement direction in the test trials
716 for all observers. Data in grey represent discrimination performance for grating
717 displacements that occurred outside the saccade execution period and colored data peri-
718 saccadic discrimination. Data in purple derive from sessions in which the grating
719 displacement occurred 35 ms after saccade initiation in the context trials and data in
720 orange from sessions with no grating displacement in the context trials. Discrimination
721 performance was quantified by the JND of the psychometric function.

722

723

724 **Figure 3**

725 **A,B** Thresholds for perceiving grating displacements - measured in the test trials - as a
726 function of time relative to saccade onset for all participants. Data shown in purple derive
727 from sessions in which the grating was displaced 35 ms after saccade onset in the context
728 trials and data shown in orange from sessions with no grating displacement in the context
729 trials.

730 **C** Average saccade peak velocities in the five sessions for saccades performed in context
731 trials (white bars) and saccades performed in test trials (blue bars). The black bar indicates
732 average data from the baseline sessions and the blue bars average data from the context
733 sessions. Error bars represent S.E.M.

734 **D** Average horizontal amplitudes in the five sessions for saccades performed in context
735 trials (white bars) and saccades performed in test trials (blue bars). Same conventions as
736 in **3C**.

737 **E** Average vertical amplitudes in the five sessions for saccades performed in context trials
 738 (white bars) and saccades performed in test trials (blue bars). Same conventions as in **3C**.
 739 **F** Saccade gain change calculated by subtracting the last ten vertical saccade amplitude of
 740 the context trials by the first ten vertical saccade amplitude of the context trials.
 741 **G** Average displacement discrimination thresholds - measured in the test trials - from
 742 baseline sessions. Data in grey represent thresholds from discrimination performance
 743 measured outside the period of saccade execution and data in red performance measured
 744 around saccade execution. Error bars represent S.E.M.
 745 **H** Average displacement discrimination thresholds - measured in the test trials - that were
 746 preceded by context trials. Same conventions as in **3G**.
 747 **I** Average motion bias - measured in the test trials - from baseline sessions. Same
 748 conventions as in **3G**.
 749 **J** Average motion bias - measured in the test trials - from test trials that were preceded by
 750 context trials. Same conventions as in **3G**.

751

752

753 **Figure 4**

754 **A** Schematic illustration of a displacement discrimination trial testing direction-specificity of
 755 the physical displacement direction. Two gratings were presented, one on the left and one
 756 on the right side of the screen. At trial start a fixation point (red color) was shown for 1000-
 757 1500 ms, then a saccade target (green color) appeared. After 60 ms both, the fixation
 758 point and the saccade target disappeared and participants were required to perform a
 759 saccade to the remembered position of the saccade target. One of the two gratings was
 760 displaced either during the saccade or after the saccade in either upward or downward
 761 direction. At the end of the trials participants had to indicate whether a displacement was
 762 seen at the left or the right side of the screen by pressing the corresponding arrow key on
 763 the computer keyboard.
 764 **B** Average displacement discrimination thresholds measured in the test trials. Bars shown
 765 in grey display average thresholds after upward displacements occurred in the test trials
 766 and white bars show thresholds after downward displacements occurred in the test trials.

767 The small colored objects indicate performance of individual participants. Error bars
768 represent S.E.M.

769

770

771 **Figure 5**

772 **A** Schematic illustration of a displacement discrimination trial testing direction-specificity of
773 the retinal motion direction. The procedure is identical to that described in Figure 4A
774 except that different gratings were used in the test trials that were displaced in upward and
775 leftward direction.

776 **B** Average displacement discrimination thresholds measured in the test trials in sessions
777 containing an upward motion context. Bars shown in grey display average thresholds after
778 upward displacements occurred in the test trials and white bars show thresholds after
779 downward displacements occurred in the test trials. The small colored objects indicate
780 performance of individual participants. Error bars represent S.E.M.

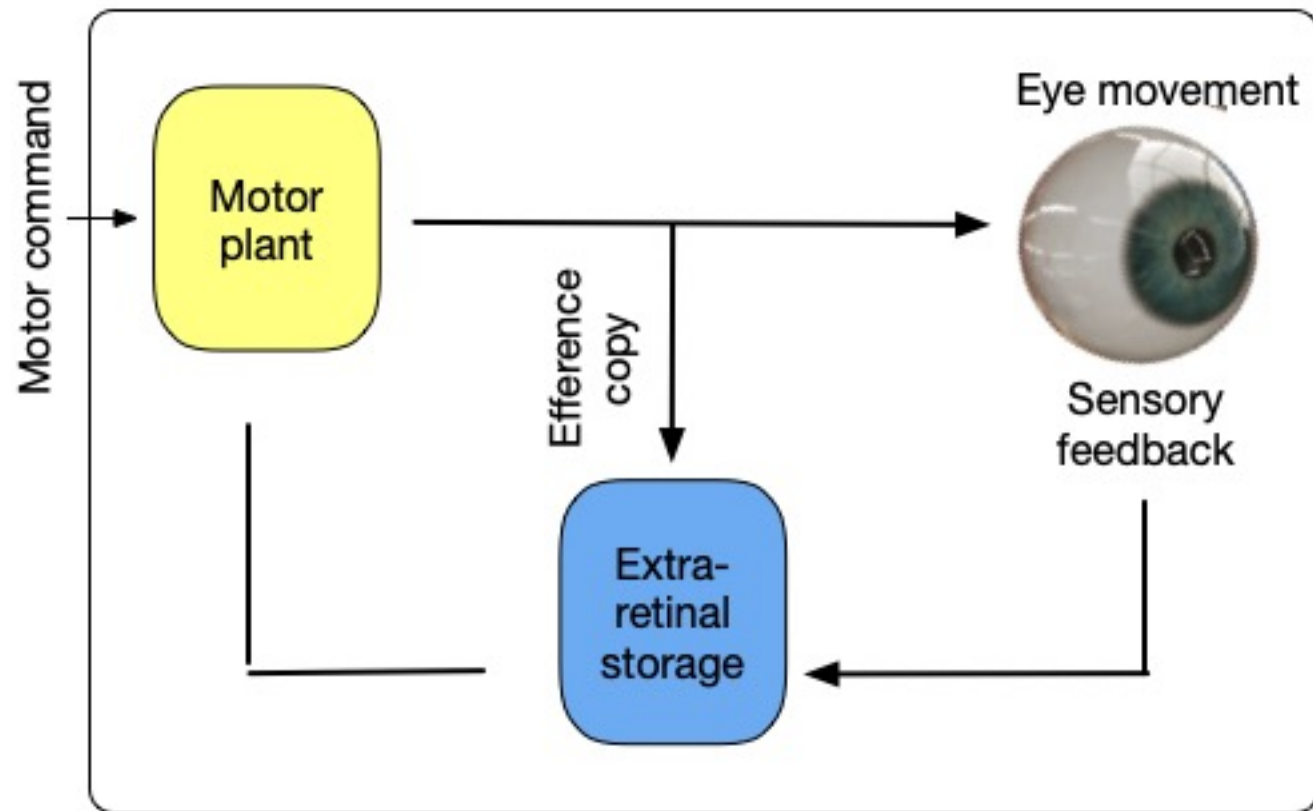
781 **C** Average displacement discrimination thresholds measured in the test trials in sessions
782 containing a downward displacement context. Same conventions as in **B**.

783

784

Figure 1

A



B

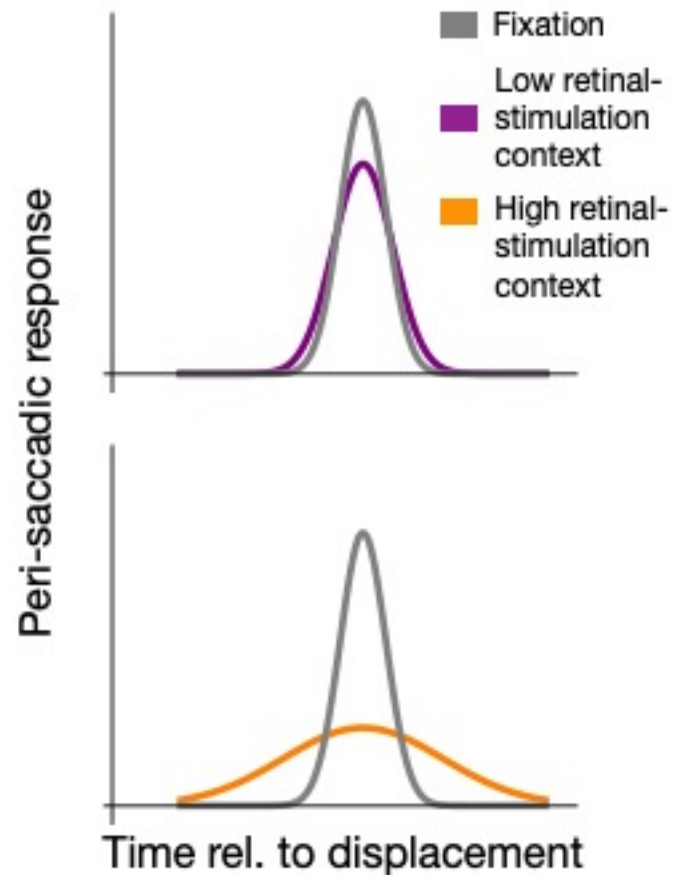
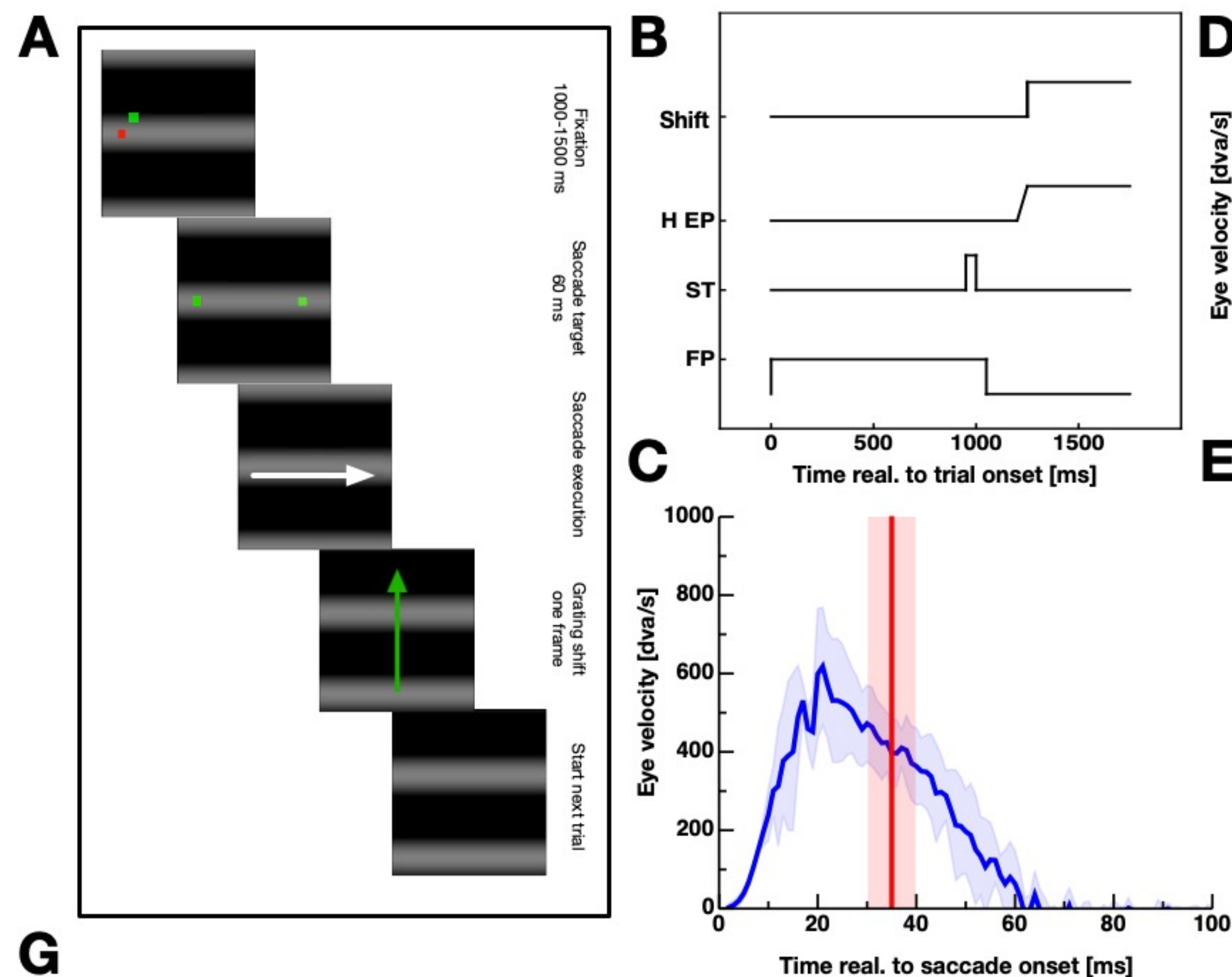


Figure 2

Context trials



Discrimination trials

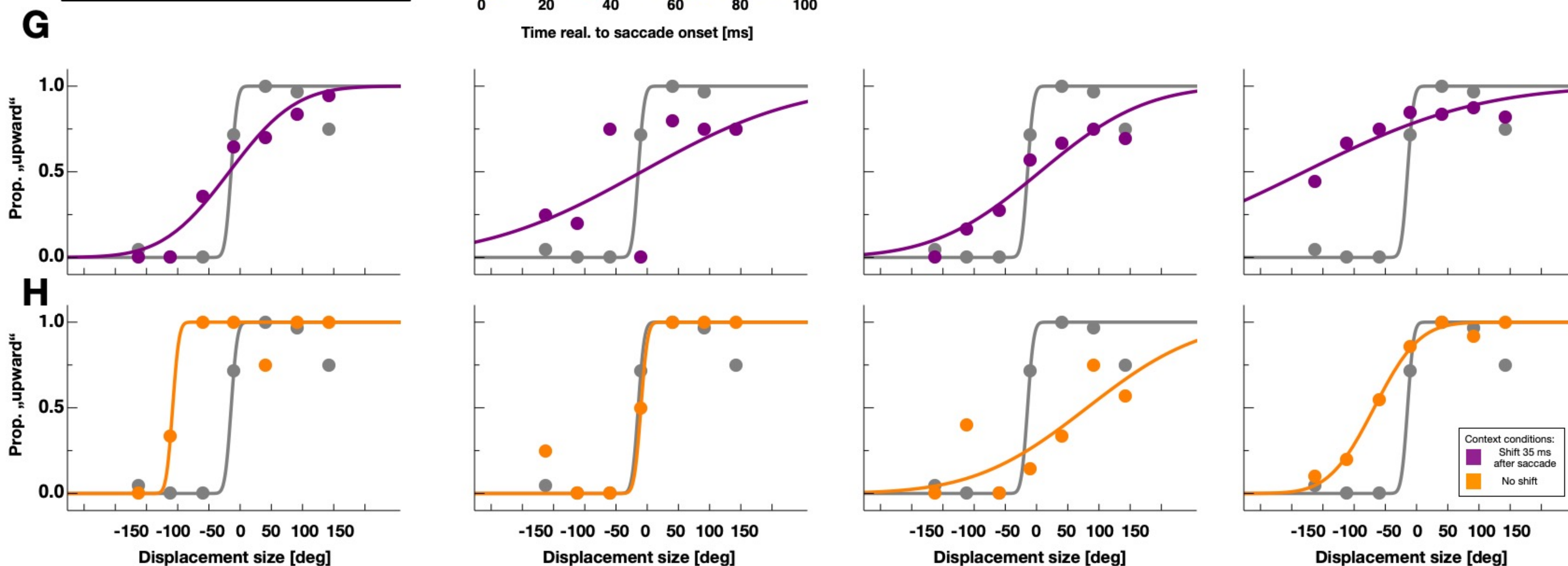
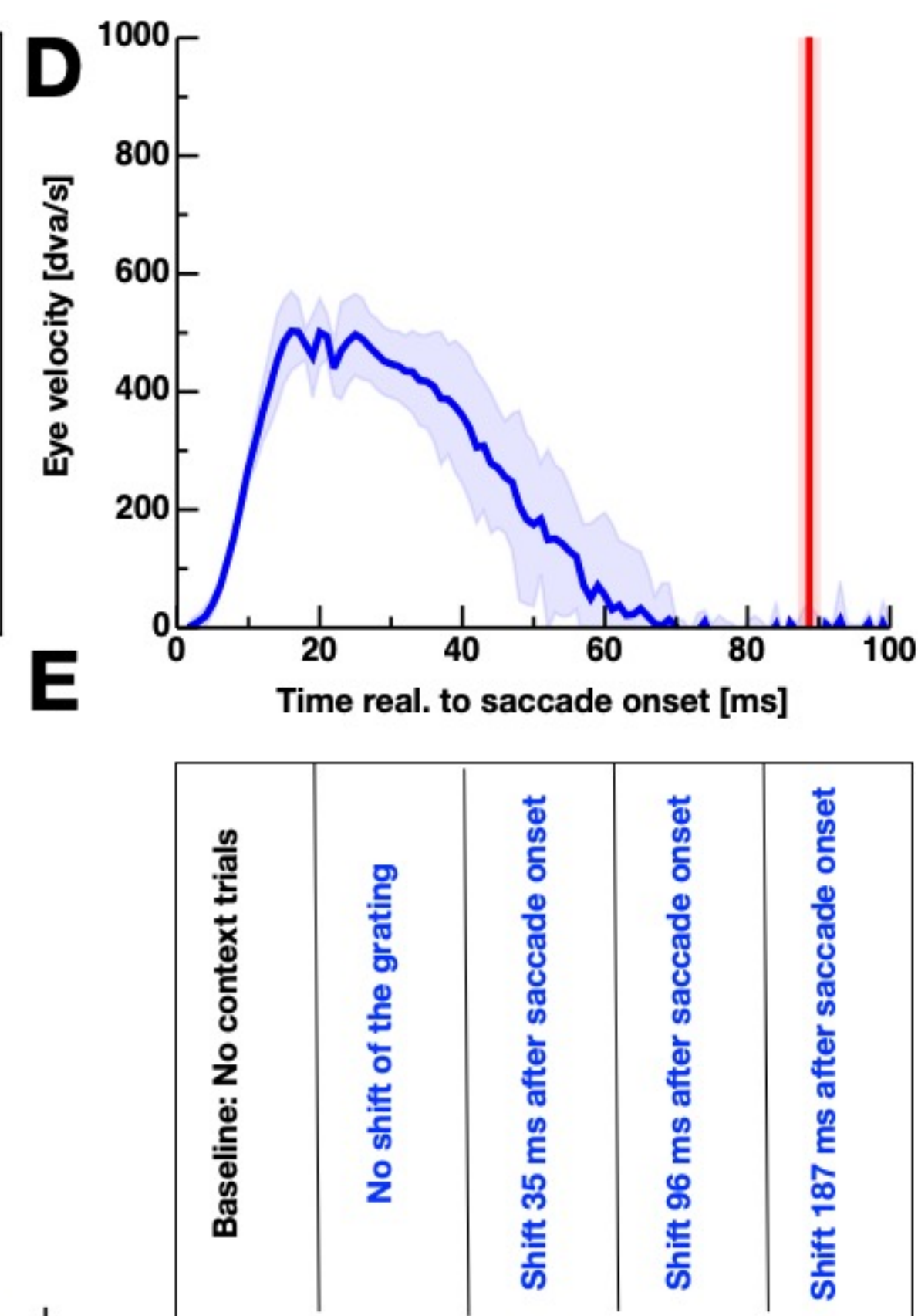
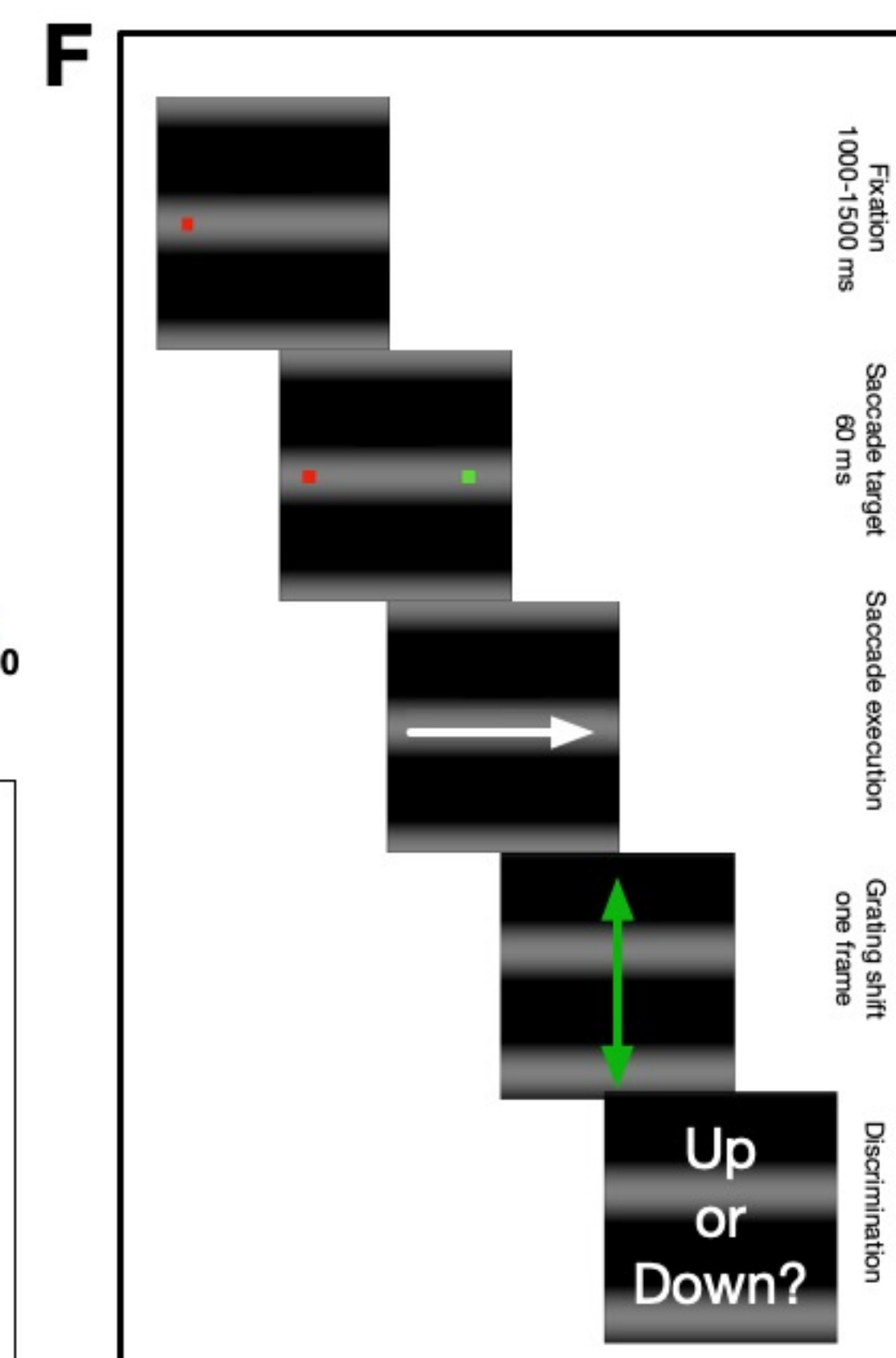


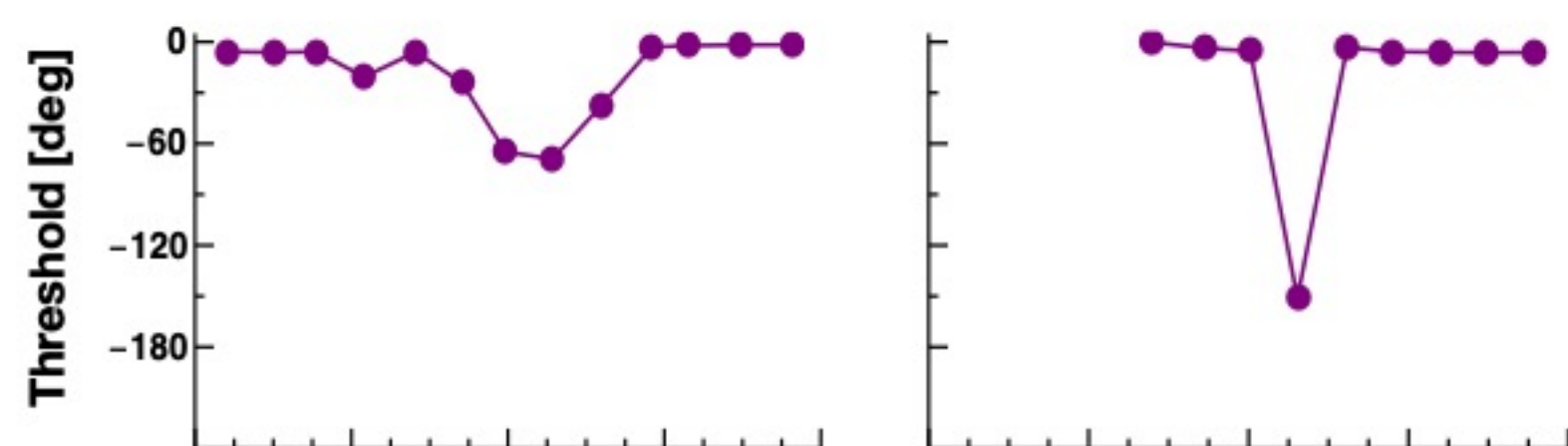
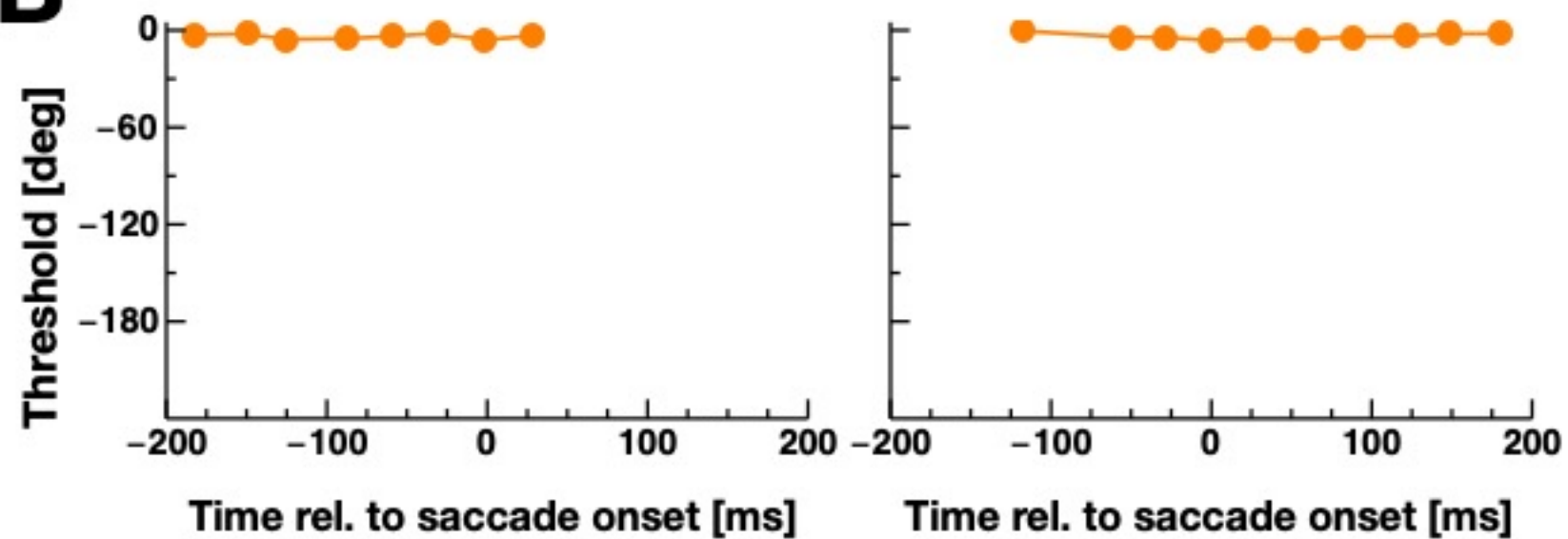
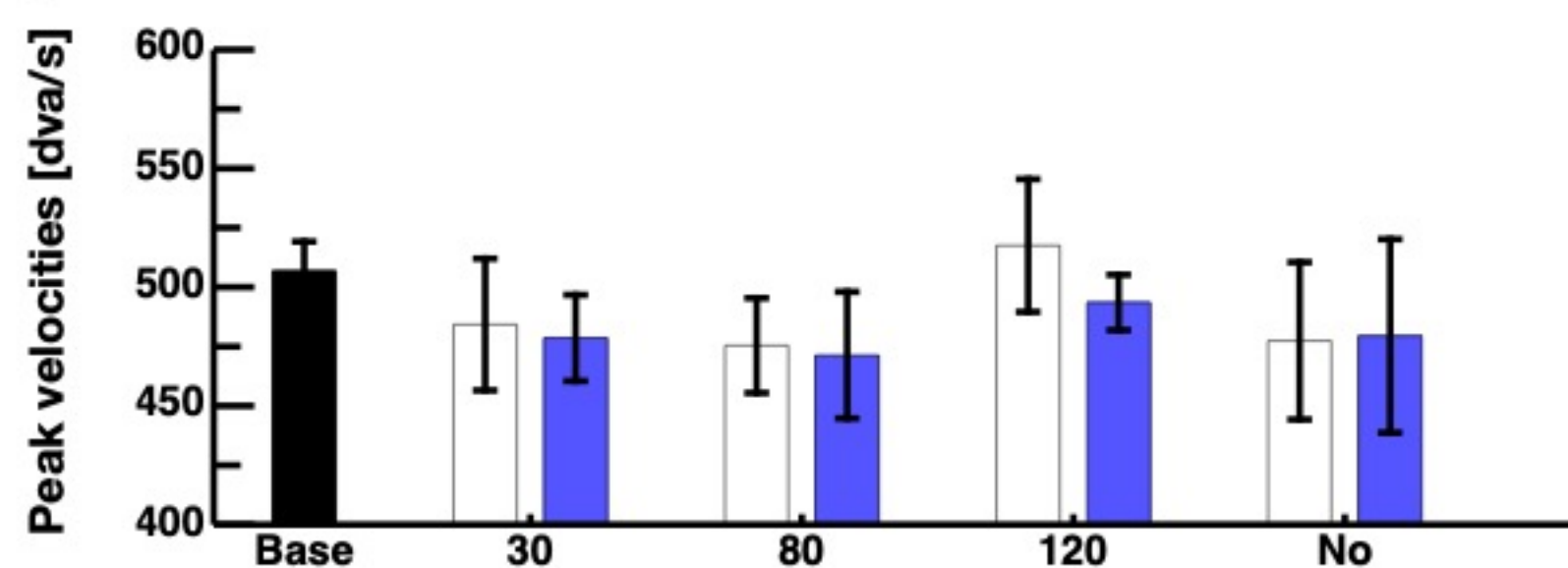
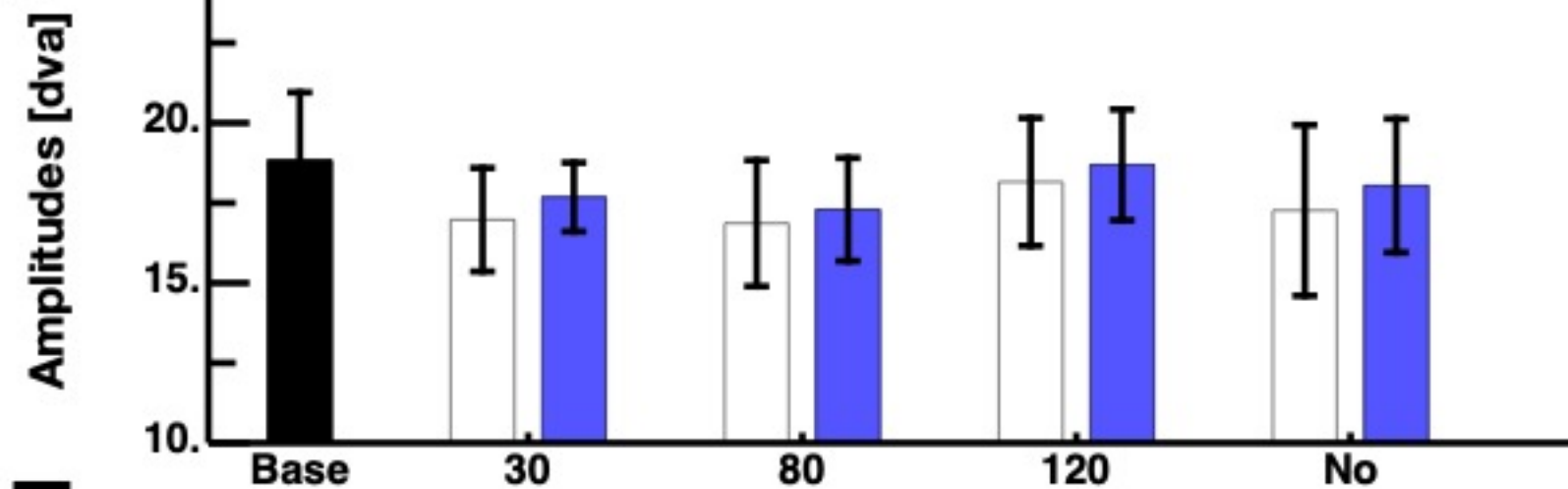
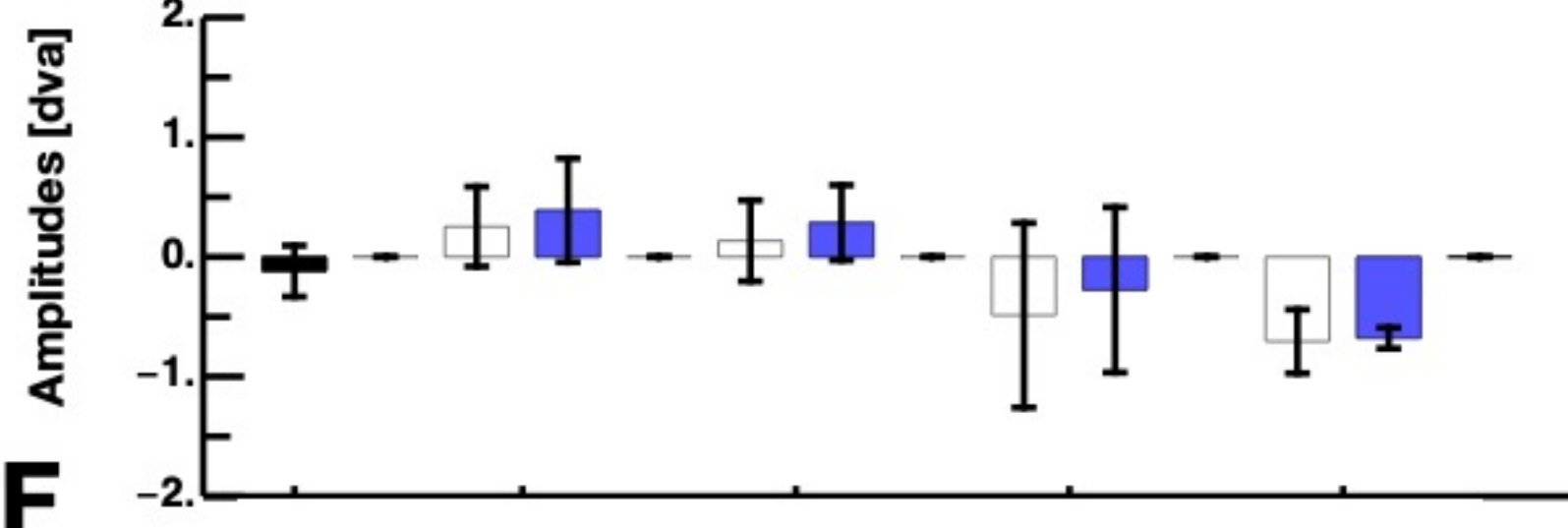
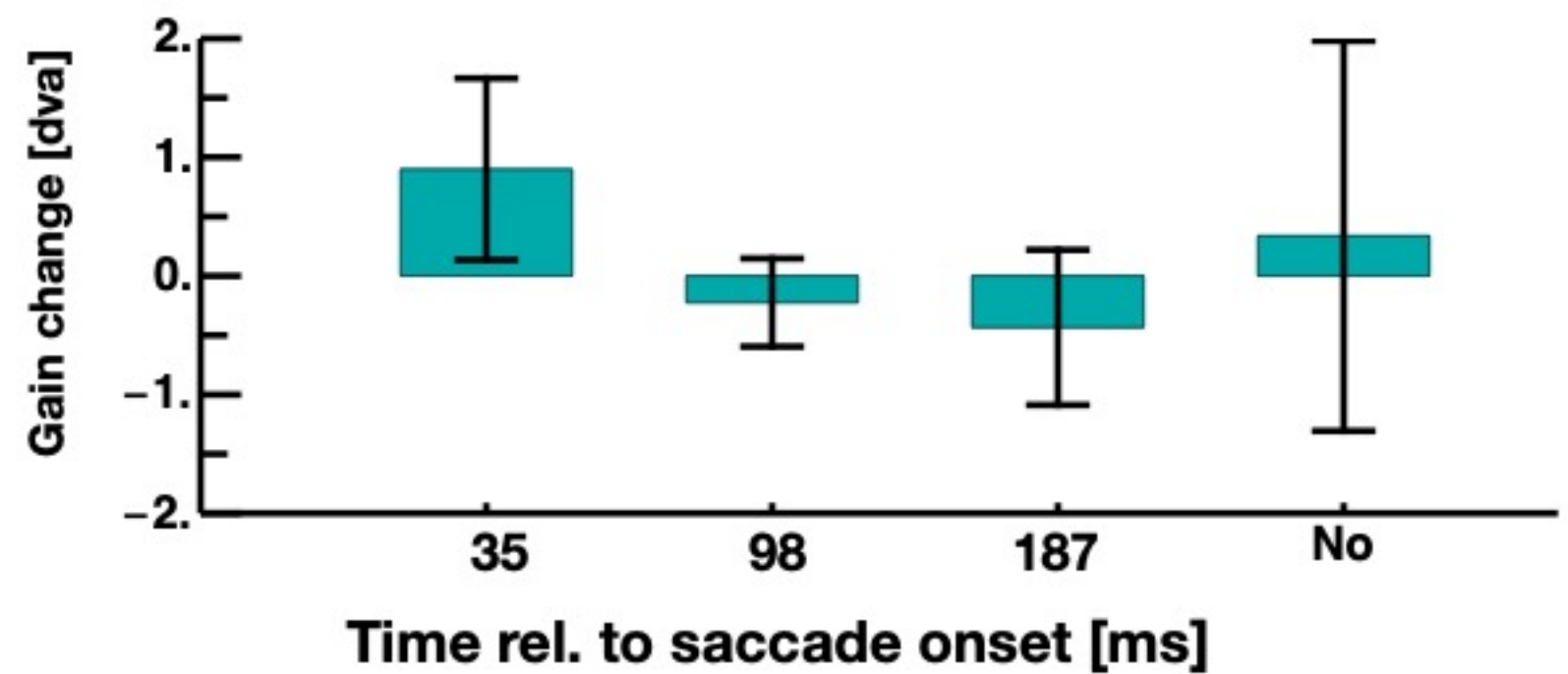
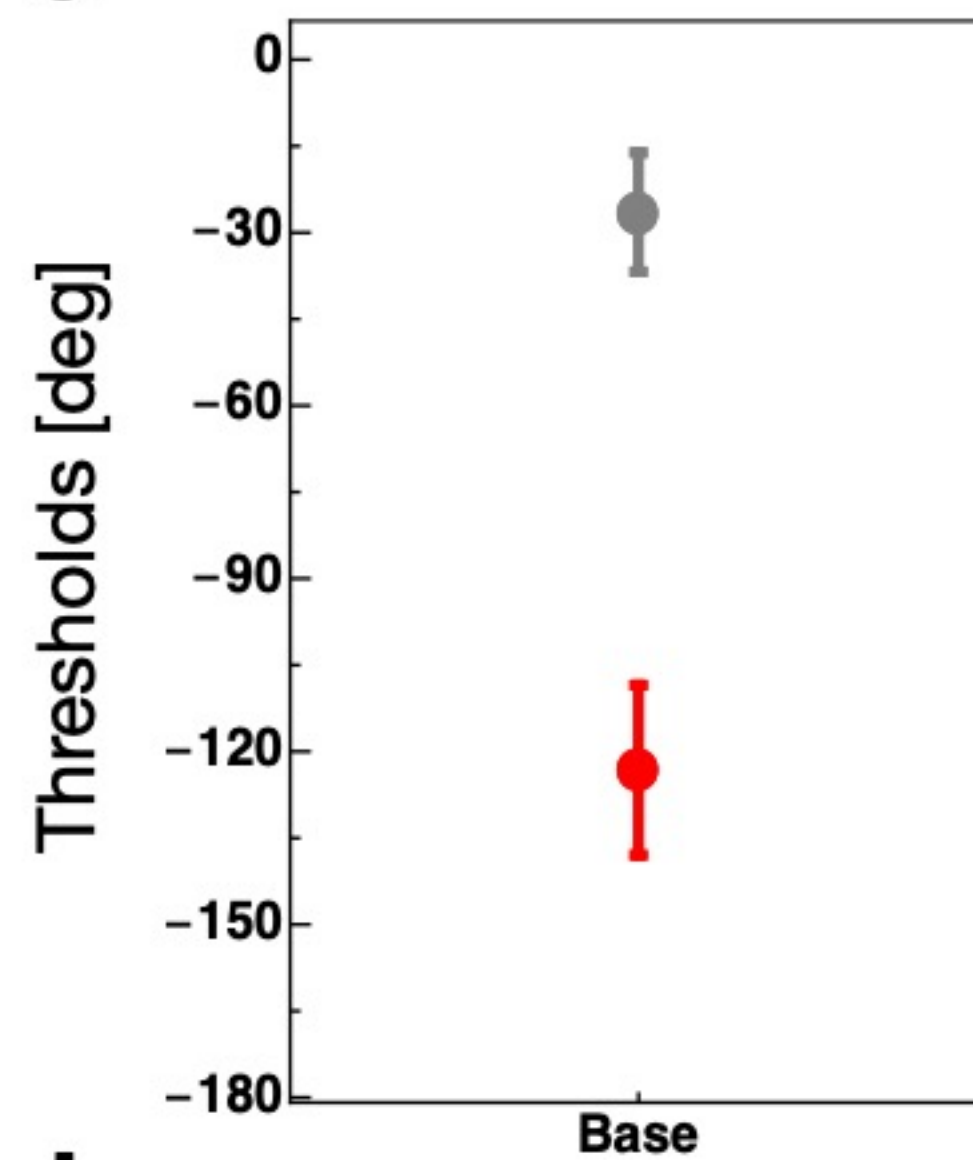
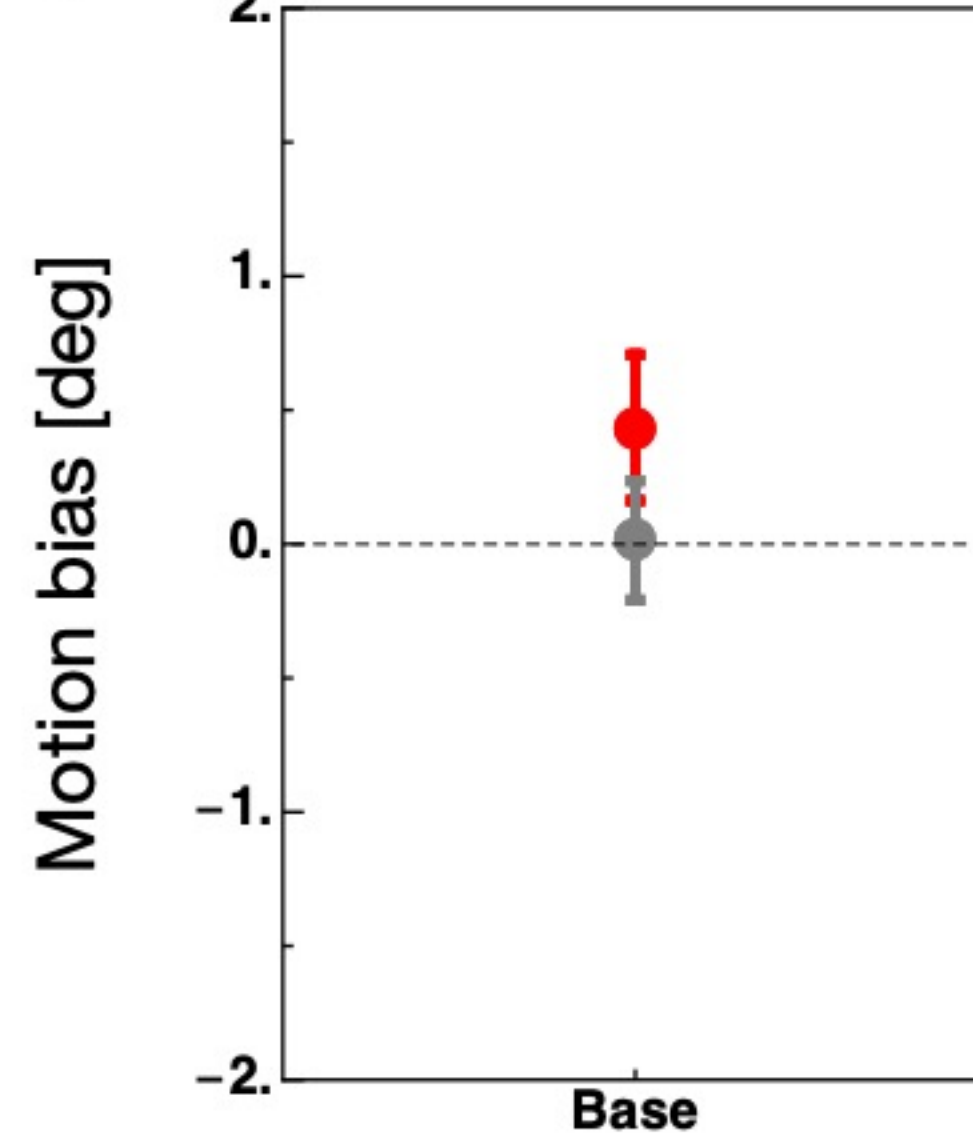
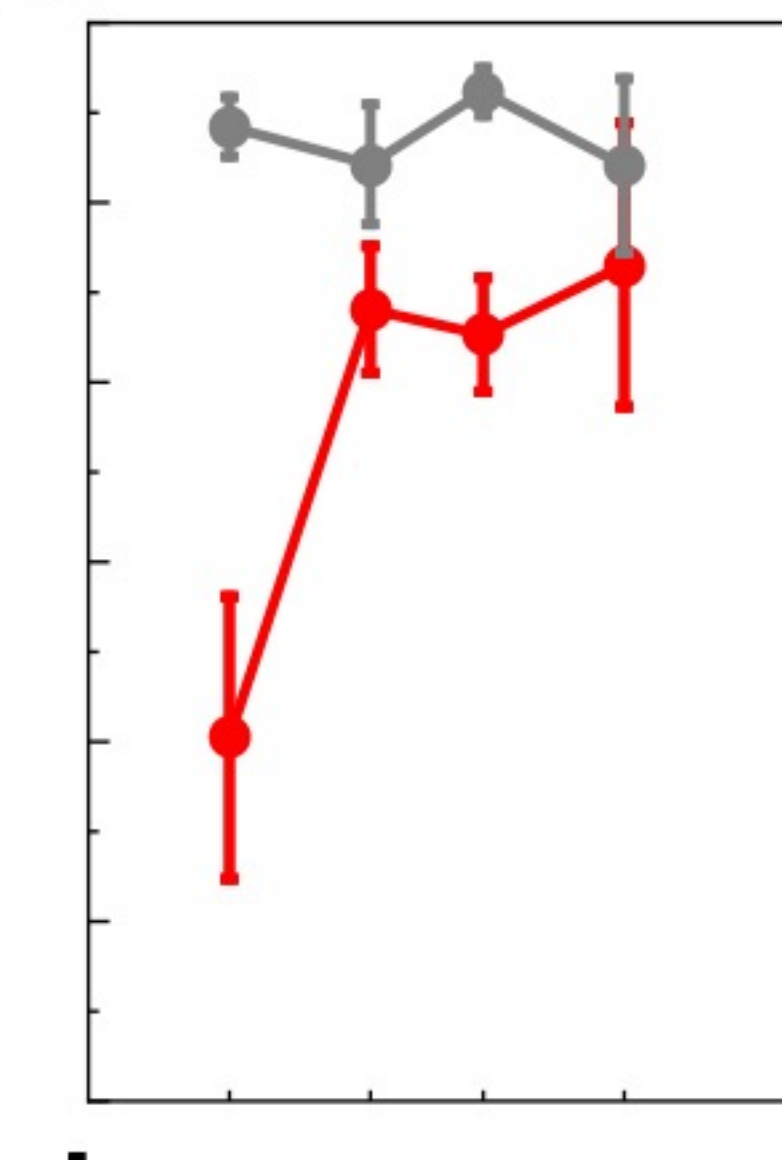
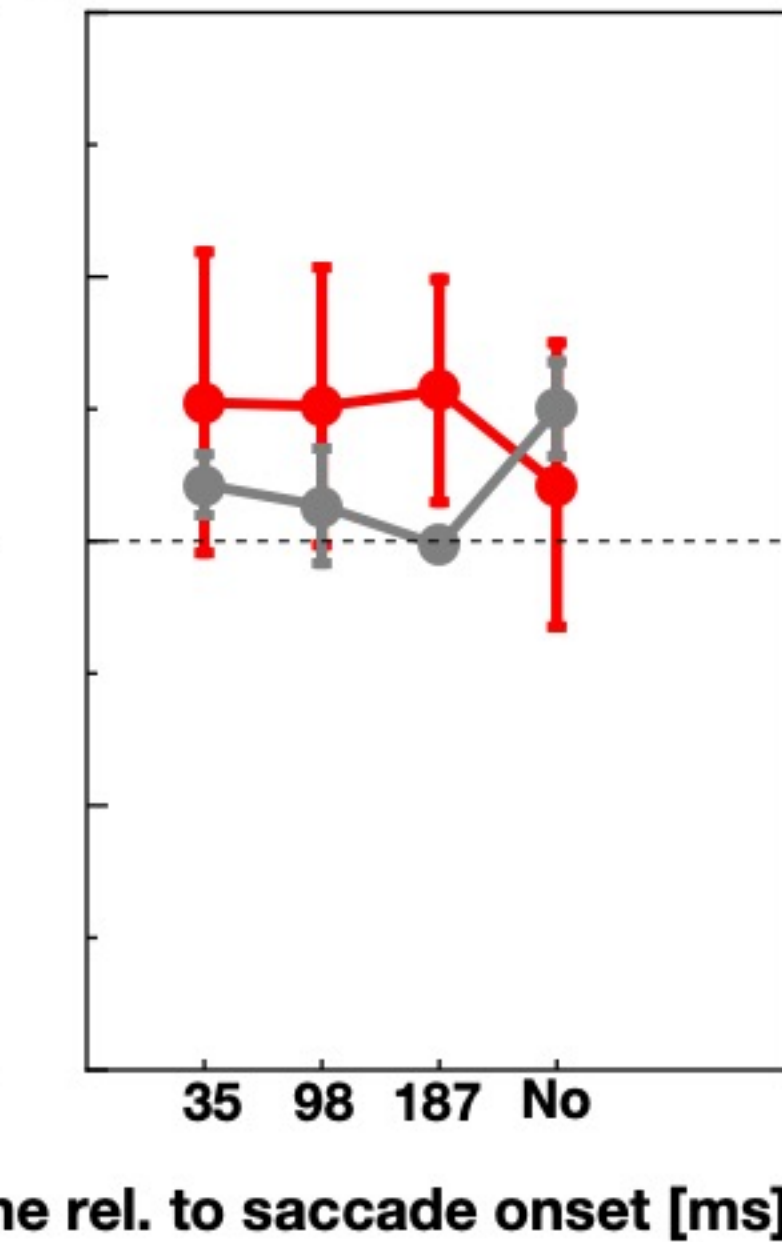
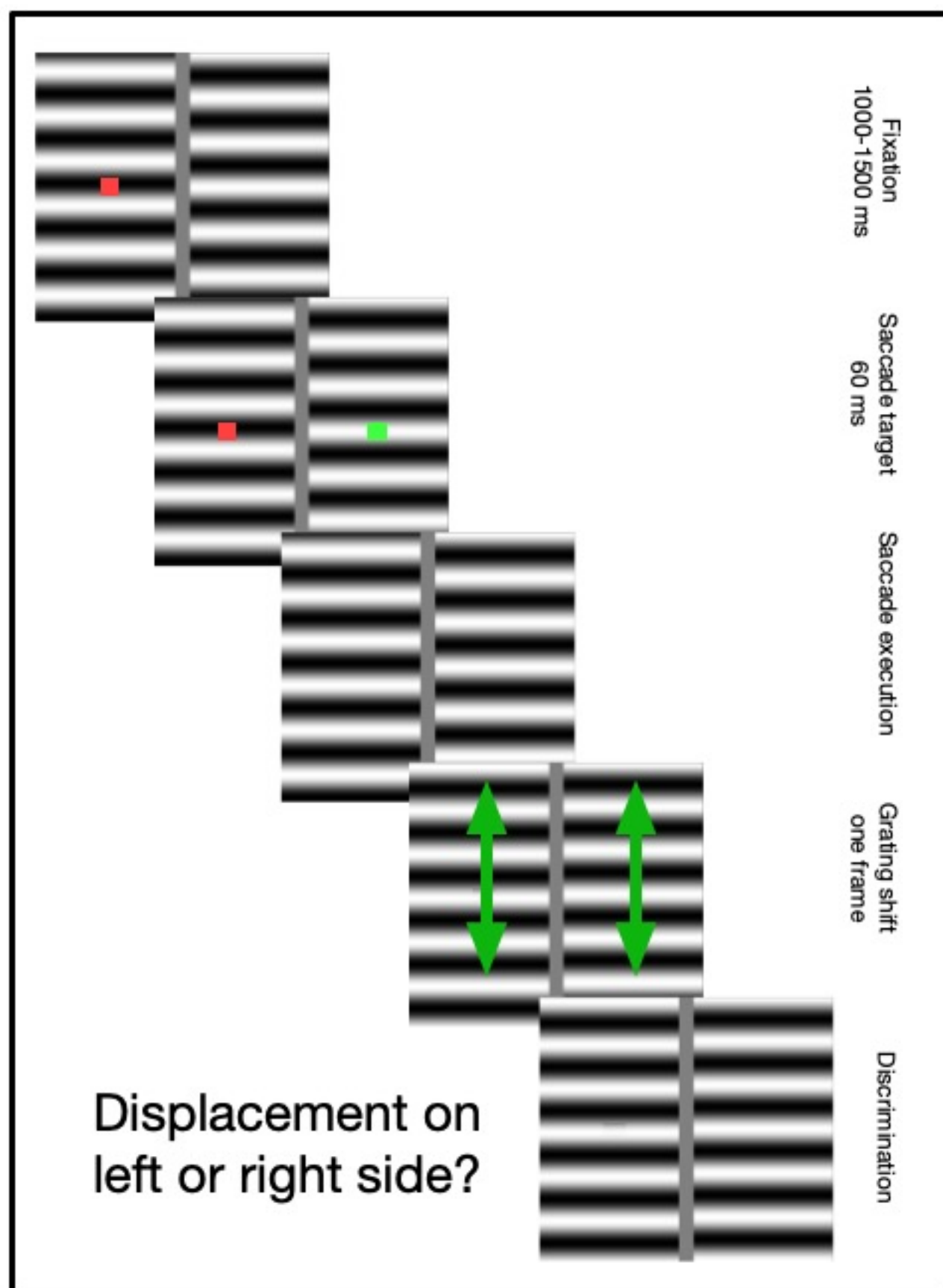
Figure 3**A****B****C****D****E****F****G****I****H****J**

Figure 4

A



B

Upward displacement context

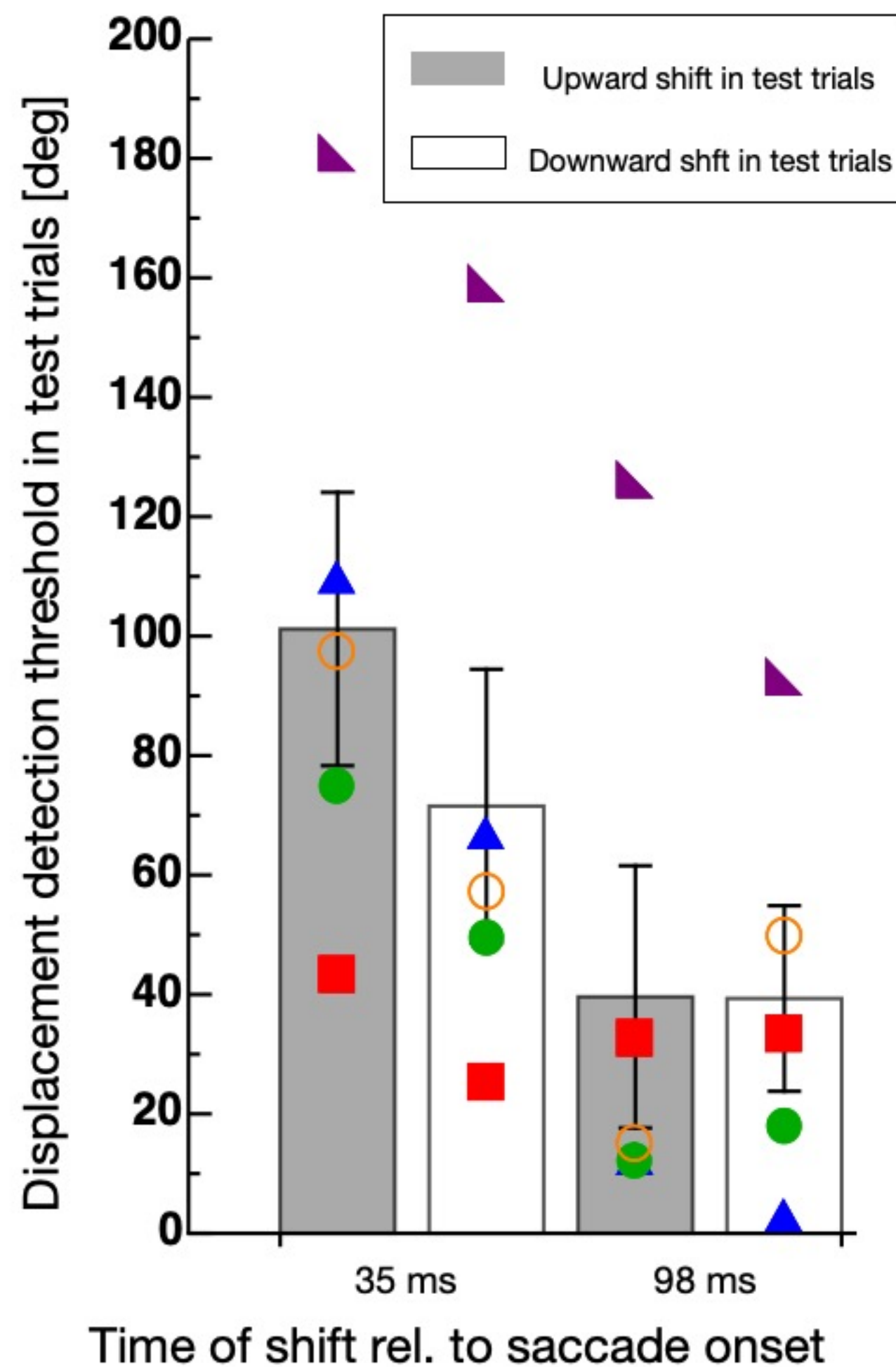


Figure 5

