Electrophysiological recordings in humans reveal reduced location-specific attentional-shift activity prior to recentering saccades

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Received October 22, 2010; Accepted December 6, 2011.

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Abstract

Being able to effectively explore the visual world is of fundamental importance, and it has been suggested that the straight-ahead gaze position within the egocentric reference frame ("primary position") might play a special role in this context. In the present study we employed human electroencephalography (EEG) to examine neural activity related to the spatial guidance of saccadic eye movements. Moreover, we sought to investigate whether such activity would be modulated by the spatial relation of saccade direction to the primary gaze position (recentering saccades). Participants executed endogenously cued saccades between five equidistant locations along the horizontal meridian. This design allowed for the comparison of isoamplitude saccades from the same starting position that were oriented either toward the primary position (centripetal) or further away from it (centrifugal). By back-averaging time-locked to the saccade onset on each trial, we identified a parietally distributed, negative-polarity EEG deflection contralateral to the direction of the upcoming saccade. Importantly, this contralateral presaccadic negativity, which appeared to reflect the location-specific attentional guidance of the eye movement, was attenuated for recentering saccades relative to isoamplitude centrifugal saccades. This differential electrophysiological signature was paralleled by faster saccadic reaction times and was substantially more apparent when time-locking the data to the onset of the saccade rather than to the onset of the cue, suggesting a tight temporal association with saccade initiation. The diminished level of this presaccadic component for recentering saccades may reflect the preferential coding of the straight-ahead gaze position, in which both the eye-centered and head-centered reference frames are perfectly aligned and from which the visual world can be effectively explored.

Keywords: eye movement, attention, electroencephalography, recentering bias, presaccadic potentials

THE EXECUTION OF EYE MOVEMENTS to objects or locations of interest is carried out by a complex network of cortical and subcortical brain regions that enables a precise alignment of the observer's...
fovea with the object of interest (for review see Sparks 2002; Wurtz and Albano 1980). In general, endogenously guided saccades have longer saccadic reaction times (SRTs) compared with saccades to salient peripheral targets (Walker et al. 2000), presumably due to the need to interpret the instructional cue. However, it has been demonstrated that a specific case of cued saccades—i.e., saccades to the center of straight-ahead gaze (referred to as primary position)—are faster than those to other locations in the gaze space (Fuller 1996; Laurutis and Robinson 1986). Neurally, self-paced saccades toward the primary position are associated with decreased cortical potentials over fronto-central and parietal recording sites compared with saccades away from it (Evdokimidis et al. 1991). Moreover, using functional magnetic resonance imaging (fMRI), we recently observed that saccadic recentering is also associated with diminished activity in the superior colliculus (SC) (Krebs et al. 2010a, 2010b), a subcortical region critically involved in saccade initiation.

The above observations are in line with the notion that the primary position represents a default gaze location in which the eye-centered and head-centered reference frames are aligned and which may therefore be preferentially coded (Durand et al. 2010; Kardamakis and Moschovakis 2009; Tatler 2007). In particular, considering that the muscle strain at the primary position is minimal compared with any other position in gaze space, it may be argued that the eyes will be “drawn” toward this default location more or less automatically, which may generally subserve a highly efficient coordination of eye and head movements (Fuller 1996; Tatler 2007). With the present study, however, we sought to provide support for the notion that this coding bias goes beyond a mere reflection of the motor properties of the oculomotor system and instead also involves differential modulations with regard to the presaccadic attentional shifts toward the future gaze location.

One phenomenon that may help to illuminate this question is the observation that attention appears to be facilitated at the goal of a to-be-executed saccade. In particular, behavioral and electrophysiological studies have demonstrated that the ability to detect and discriminate peripheral targets at a particular spatial location is facilitated just before a saccade is executed to that location (Deubel and Schneider 1996; Godijn and Pratt 2002; Kowler et al. 1995; Remington 1980). Importantly, this enhancement seems to depend on a close temporal relationship between target onset and saccade execution, because attentional facilitation is only observed very briefly prior to the actual saccade execution rather than immediately following the cue (Stelmach et al. 1997). On the basis of these observations, the presumed attentional shift that precedes saccade execution has been interpreted as being an “advance scout” (Wright and Ward 2008) or “attentional pointer” (Cavanagh et al. 2010) that guides the eye movement to the location of interest and provides an attentional preview of the future gaze location.

Regarding the neural correlates of such an “attentional scout,” animal electrophysiology studies have demonstrated that neurons in key saccade-processing regions, in particular in the SC in the brain stem and the lateral intraparietal (LIP) area in the cortex, exhibit increased responses shortly before saccade initiation that are distinguishable from the neural signatures of actual saccade execution (e.g., Duhamel et al. 1992; Goldberg and Wurtz 1972; Lynch and McLaren 1989). More specifically, the presaccadic activity of LIP neurons has been proposed to reflect “anticipatory” visual-field shifts that allow for a stable representation of the visual world immediately after the saccade—without any delay related to the signal transmission from the retina (Cavanagh et al. 2010; Colby et al. 1995; Duhamel et al. 1992; Kusunoki and Goldberg 2003). In humans, in addition to the well described EEG premotor potentials over fronto-central recording sites that appear to be related to the actual eye movement generation (see, e.g., Klostermann et al. 1994; Thickbroom and Mastaglia 1985), other more recent studies have linked presaccadic cortical potentials over occipito-parietal sites to attentional-orienting processes (Clementz et al. 2007; Gutteling et al. 2010; Luck et al. 1997; van der Lubbe et al. 2006; Wauschkuhn et al. 1998). However, establishing that these activation patterns
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Saccadic reaction time analysis. Cue-locked analysis.

Timing of cue onsets was randomly varied with a stimulus onset asynchrony (SOA) between 1,000 and 1,500 ms. The design resulted in eight saccade conditions (Fig. 1B), along with the maintain-fixation condition in which an instructional cue was presented but no eye movement was performed.

Prior to the actual EEG experiment, participants performed a 10-min training session to become familiarized with the task. The actual study was performed in a sparsely lit electrically shielded chamber. The EEG was recorded from 64 electrodes mounted in a custom-designed electrocap (Electro-Cap International, Eaton, OH) and referenced to the right mastoid during recording. Electrode impedances were maintained below 2 kΩ for the mastoids, below 10 kΩ for the electrooculogram (EOG) electrodes, and below 5 kΩ for all remaining electrodes. All 64 EEG channels were continuously recorded with a band-pass filter of 0.01–100 Hz at a sampling rate of 500 Hz (SynAmps amplifiers from Neuroscan). In addition, a noncausal, zero-phase, running-average filter of 9 points was applied off-line, which strongly reduces frequencies at and above 56 Hz at our sampling frequency of 500 Hz. Eye movements and blinks were recorded by horizontal and vertical EOG electrodes for the rejection of blink artifacts, as well as for the subsequent analyses of saccade onset and saccade direction. Participants’ fixation performance in the saccade task was additionally monitored online via a video camera in the EEG chamber.

Participants performed eight 4-min experimental runs, yielding a total of 160 trials in each saccade condition (Fig. 1B): left and right 1-to-0 centripetal (recentering), left and right 0-to-1 centrifugal, left and right 1-to-2 centrifugal, and left and right 2-to-1 centripetal, plus a total of 70 maintain-fixation trials (i.e., 14 trials at each of the 5 squares). Importantly, the design allowed us to compare specific centripetal and centrifugal saccades (1-to-0 centripetal vs. 1-to-2 centrifugal) with identical shift amplitudes and identical directional probabilities (i.e., the shift direction was equally predictable) that started at identical distances from the primary position (as illustrated in Fig. 1C). Thus these saccade types differed only in the orientation (centripetal vs. centrifugal) of the movement with respect to the primary position, allowing for a particularly clean investigation of the neural correlates associated with the recentering bias. The additional saccade conditions (see Fig. 1B: 0-to-1 centrifugal and 2-to-1 centripetal) were required to provide equal directional probabilities throughout the task but were not included in the main analysis.

**Saccadic reaction time analysis.** Saccade onsets were determined based on the horizontal EOG channels with a built-in template-matching routine implemented in the Brain Vision Analyzer 1.05 software package (Brainproducts, Munich, Germany). In particular, markers were positioned right before the saccade-related vertical amplitude shift (see Fig. 3, bottom). Latencies were calculated as the difference between cue onset and the onset of correctly executed saccades based on the EOG saccade-onset markers. SRTs and accuracy data from all saccades with a minimum latency of 200 ms were averaged for the conditions of interest (left and right 1-to-2 centrifugal and left and right 1-to-0 centripetal) and analyzed via repeated-measures analysis of variance (rANOVA) with factors saccade direction (left vs. right) and saccade orientation (centrifugal vs. centripetal).

**Cue-locked analysis.** To investigate the early event-related potential (ERP) components that are related to processing of the visual cue itself and the associated early attentional orienting, the ERP data were analyzed time-locked to the onset of the color cue. After artifact correction (i.e., rejecting trials with blinks or muscle activity), data were averaged separately for each saccade condition of interest into 600-ms epochs that included a 200-ms precue segment and a 400-ms postcue segment. It should be noted that for the cue-locked analysis only trials with saccade latencies larger than 400 ms were included in order to allow for the development of early ERP components typically associated with instructional cues in the absence of saccade-related activity. Accordingly, a saccade-independent interpretation of cue-related activity was only feasible within the first 400 ms after cue. The
time-locked average ERP responses were baselined with respect to the 200-ms precue segment. To investigate potential general activity differences associated with the processing of directional cues between the conditions of interest (1-to-0 centripetal and 1-to-2 centrifugal), the ERP responses were collapsed across left and right cues within each condition. After the rejection of blinks and muscle artifacts, erroneous saccades, and saccades with SRTs below 400 ms, the average number of trials per participant in this analysis was 169 for 1-to-2 and 156 for 1-to-0 saccades. For both of these conditions, <10% of trials needed to be excluded because of artifacts. Spherical spline-interpolated topographic voltage maps were derived across participants for a series of consecutive 20-ms windows between 180 and 380 ms after cue in order to visualize the activity distribution of the cuing conditions of interest (Fig. 2A). Paired t-tests were performed comparing peak amplitude values of the conditions of interest over all sampling points within sequential windows of 20 ms between 200 and 240 ms and between 340 and 380 ms after cue at centro-parietal electrodes (Cz, CPz) selected based on the topographic difference maps (Fig. 2A, bottom). The time points between 380 and 400 ms were not considered for the analysis because of possible filter-induced contributions from the spike potential associated with the saccade onsets that could occur around 400 ms.

**Saccade-locked analysis.** On the basis of the EOG saccade onset markers, the data were segmented time-locked to saccade onset into 1,000-ms epochs that included a 800-ms presaccade period and a 200-ms postsaccade period, positioning saccade onsets at time zero. After rejection of epochs that included blinks, muscle artifacts, or erroneous saccades, data were averaged separately for each saccade condition of interest (left and right 1-to-2 centrifugal and left and right 1-to-0 centripetal). Data were baselined with a window between −800 and −600 ms before saccade, a period that preceded the cue presentation while also not including any saccade-related activity from the preceding trial. Similar to the cue-locked analysis, activity was collapsed across leftward and rightward saccades within each condition of interest (1-to-2 centrifugal and 1-to-0 centripetal). After rejection of artifacts and erroneous saccades, the average number of trials per participant in this analysis was 285 for 1-to-2 saccades and 284 for 1-to-0 saccades. For both conditions, <10% of trials needed to be excluded because of artifacts. Topographic voltage maps were derived for a series of consecutive 20-ms windows between −200 ms and time zero (saccade onset) to compare conditions of interest (Fig. 2B). Separate paired t-tests were computed for sequential windows of 20 ms between −60 and −20 ms prior to saccade onset at centro-parietal peak-amplitude electrodes (Cz, CPz) selected based on the topographic difference maps (Fig. 2B, bottom). Although included in the topographic plot, the time points between −20 ms and time zero were not considered for the analysis, to avoid any possible contributions from the saccadic spike potential.

**Analyses of contralateral versus ipsilateral activity.** In addition, in order to investigate neural components that are specifically linked to the deployment of spatial attention, cue-locked and saccade-locked data were collapsed across left and right saccade conditions to represent contra- and ipsilateral activity changes for each condition of interest (contralateral: left hemisphere activity preceding rightward saccades and right hemisphere activity preceding leftwards saccades; ipsilateral: vice versa). Separate rANOVAs with factors contralaterality (contra- vs. ipsilateral) and saccade orientation (centrifugal vs. centripetal) were performed for data averaged over all sampling points (sequential windows of 20 ms) at the respective peak-amplitude electrodes. Based on the topographic distributions, the cue-locked analysis was performed between 280 and 380 ms after cue (PO7), while saccade-locked data were analyzed between −120 and −20 ms prior to saccade onset (PO3).

To test whether the observed differences between centrifugal and centripetal saccades would be related to a more frequent overlap between the visual offset of the cue at 300 ms and saccade onset in the centripetal condition, we performed an analogous saccade-locked analysis incorporating only saccades with a minimum SRT of 400 ms. In this trial selection, the neural response to the cue offset...
Saccadic reaction times. The behavioral and EEG analyses were restricted to the key conditions of interest (i.e., left and right 1-to-2 centrifugal, left and right 1-to-0 centripetal), since only these saccades were matched for shift amplitude, directional probability, and starting position. The latency distribution of correctly executed saccades in both conditions of interest ranged between 200 and 600 ms, which is in the typical range for endogenously cued saccades (Walker et al. 2000). In terms of accuracy, participants consistently performed saccades in the cued direction, as indicated by a mean percentage of correct saccades of 99% in the conditions of interest. No significant differences in accuracy were observed between the key conditions (1-to-2 centrifugal = 0.989, 1-to-0 centripetal = 0.994; \( P = 0.09 \)).

The rANOVA of SRTs with factors saccade direction (leftward/rightward) and saccade orientation (centrifugal/centripetal) revealed a significant main effect of saccade orientation, indicating that centripetal recentering saccades were indeed facilitated compared with the matched centrifugal saccades [mean ± SE SRT: 1-to-2 centrifugal = 421 ± 9.4 ms, 1-to-0 centripetal = 413 ± 9.8 ms; \( F_{(1,15)} = 11.46, P = 0.004 \); Fig. 1C, top]. It should be noted that, considering the repeated-measures nature of the analysis, the actual tests of differences between the within-subject means are based on the standard error of the difference between each pair. The SRT distributions of the conditions of interest (Fig. 1C, bottom) furthermore indicate that the recentering bias was consistent across different SRT windows between 200 and 600 ms. No main effect of saccade direction was observed between left- and rightward saccades (\( P > 0.3 \)), and there was no interaction between saccade direction and saccade orientation (\( P > 0.8 \)).

Cue-related activity. Cue-related activity for the key conditions, collapsed across left and right saccade directions, is shown between 180 and 380 ms after cue in Fig. 2A. Both centrifugal and centripetal cue types were associated with a bilateral occipital negative deflection and a strong fronto-central positivity (starting around \( \sim 180 \) ms), followed by a later centro-parietal positivity (starting around \( \sim 320 \) ms) that led up to the eye movement itself. These topographic distributions of the cue-related neural activity preceding 1-to-2 centrifugal and 1-to-0 centripetal saccades from position 1 appeared to be highly similar. Consistent with this impression, testing for possible amplitude differences over central scalp sites (electrodes Cz and CPz) did not yield significant differences between these two cue conditions (paired \( t \)-tests for the four 20-ms windows between 200 and 240 ms and between 340 and 380 ms: all \( P \) values > 0.3). Time points later than 380 ms after cue were not considered in the analysis because of the potential overlap with saccadic spike potentials associated with saccade onset at \( \sim 400 \) ms after cue.

Given the contralateral representation of the attentional focus and saccade targets in various visual processing regions, the presaccadic attentional employment would be expected to follow the same contralateral mapping. Hence, to investigate the direction-specific neural activity in response to the directional cue, data from left and right cues were combined to represent activity contra- and ipsilateral to the direction indicated by the cue. The resulting topographic distributions are shown in Fig. 3A for the conditions of interest, with contralateral activity represented over the left hemisphere and ipsilateral over the right hemisphere. We observed a negative deflection contralateral to the upcoming saccade direction, which started \( \sim 280 \) ms after cue onset and was focused over parietal/occipital cortex. This contralateral negative deflection resembled the early directing attention negativity (EDAN), a posterior ERP component that has been observed between 200 and 400 ms after...
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With the present study we sought to investigate cortical activity preceding endogenously cued saccades, with a special focus on the recentering bias that has been described behaviorally (Fuller 1996) and with fMRI (Krebs et al. 2010a). We hypothesized that, in addition to being faster than other saccade types, recentering saccades would be characterized by differential neural modulations prior to the actual saccade onset. More specifically, consistent with anticipatory attentional deployment at the future gaze location that helps to guide the saccade, we expected enhanced presaccadic activity over posterior sites contralateral to saccade direction. Moreover, we hypothesized that this contralateral enhancement would be smaller prior to recentering saccades, reflecting a diminished need for attentional guidance for saccades that return the gaze to the default coordinate of the head-centered space. Importantly, the present design enabled us to compare centripetal recentering saccades (1-to-0) to centrifugal saccades (1-to-2) that were matched for starting position, amplitude, and directional probability.

In line with the notion of a behavioral facilitation toward the primary position, we observed shorter SRTs for centripetal saccades, as previously reported in both animals (McIlwain 1986) and humans (Fuller 1996; Laurutis and Robinson 1986). Although the absolute size of the SRT modulation was relatively small, it was very consistent across participants as well as across different SRT ranges and similar to earlier reports of this effect considering the relatively small saccade amplitude of 7° (Fuller 1996).

In our electrophysiological measures of the neural activity that directly preceded the eye movement in the saccade-locked analysis, we observed a negative deflection contralateral to saccade direction over posterior electrode sites. Importantly, this presaccadic contralateral component was significantly modulated by the saccade orientation relative to the primary position. Specifically, the contralateral negativity started later and was of significantly smaller amplitude prior to recentering saccades compared with centrifugal saccades starting from the same position. While several previous reports on saccade processing reported similar presaccadic posterior components, these were not independent of exogenous attentional capture or additional task requirements (e.g., Gutteling et al. 2010; Wauschkuhn et al. 1998). On the other hand, one saccade study failed to observe an analogous component directly preceding the eye movement (van der Lubbe et al. 2006). That study, however, employed a delayed-saccade task, thereby emphasizing the advance coding and maintenance of the future saccade goal throughout the delay, which is in contrast to the present study in which subjects were instructed to saccade right away in response to the instructional cue, likely accounting for the differences in the observed saccade-locked components.

Of note, although a similar contralateral activity modulation was observed in the present cue-locked analysis, this effect was much weaker compared with the saccade-locked data, suggesting that the presaccadic modulation is temporally more closely linked to saccade execution than to the processing of the instructional cue. Importantly, participants were instructed to immediately move their eyes to the new location upon the color change, which might have caused the cue-induced attentional shift and the actual saccade initiation to overlap substantially. Therefore, the possibility that the observed cue-locked effect is simply a washed-out version of the presaccadic contralateral enhancement, which was indeed much stronger, cannot be ruled out on the basis of the present data. Thus the question as to whether the recentering bias would also be preserved in a purely covert version of the present paradigm remains to be addressed in future studies.

The observation of a presaccadic posterior component is consistent with behavioral reports of facilitated stimulus processing at the prospective saccade end point that arises only briefly before saccade execution (Deubel and Schneider 1996; Godijn and Pratt 2002; Kowler et al. 1995; Stelmach et al. 1997), an observation that contributed to the notion of a presaccadic attentional scout in the
first place (reviewed in Wright and Ward 2008). It should be emphasized that the present paradigm did not involve an additional task at the future gaze location (e.g., Gutteling et al. 2010) nor, and probably more importantly, any salient peripheral events (e.g., Wauschkuhn et al. 1998). Specifically, the peripheral visual input was completely static and did not change between the onset of the cue and the onset of the saccade, which is the time period in which the differential contralateral negativity was observed. We thus believe that, rather than being the consequence of any attentional capture or subsequent target processing in the periphery, the presaccadic activity modulation observed here provides evidence for some sort of attentional-scout process that immediately precedes and helps to guide the eye movement itself.

It has been suggested that such an attentional scout is useful or even necessary in natural vision for perceptual stability across eye movements (e.g., Cavanagh et al. 2010; Colby et al. 1995). Specifically, presaccadic “anticipatory” visual field shifts are thought to provide a preview of the future visual input to allow for maintaining a stable representation of the visual world immediately after the saccade—without any delay related to the signal transmission from the retina (Cavanagh et al. 2010; Kusunoki and Goldberg 2003). Such visual-field shifts have been related to presaccadic activity modulations in posterior cortical regions, namely, in LIP (Colby et al. 1995; Duhamel et al. 1992; Kusunoki and Goldberg 2003), as well as in area V4 (Moore and Chang 2009). Both the topographic distribution and the timing of the presaccadic effect in the present data are consistent with such an anticipatory attentional shift toward the future gaze location.

Moreover, from a human ERP perspective, the observed presaccadic activity over parietal/occipital sites in the cue-locked and saccade-locked analyses nicely matches the topographic distribution of two well-described ERP components related to location-specific attentional orienting. In particular, the presaccadic contralateral effect had a distribution similar to the negative-polarity, posteriorly distributed ERP wave known as the EDAN that has been proposed to reflect activity related to a covert attentional shift toward a cued location (e.g., Hopf and Mangun 2000). Consistently, the differential presaccadic modulations in the present study were exclusively observed when comparing contralateral and ipsilateral activity with respect to saccade direction, while they were absent in the general direction-unspecific activity levels (Fig. 2), underscoring the location-specific nature of this component. Likewise, the distribution of the presaccadic component was also very similar to the N2-posterior-contralateral (N2pc) component, which is a contralateral enhanced negativity at posterior electrodes (Luck 1994). This component is typically observed in visual-search paradigms and is thought to index the allocation of covert attention to a peripheral target (Cohen et al. 2009; Hopf et al. 2000; Luck 1994). Despite the different paradigmatic approaches, the EDAN and the N2pc may reflect a shared mechanism of spatial attentional orienting. Moreover, it has been argued that the EDAN might actually reflect an N2pc-like attentional capture by lateralized aspects of the cue itself, rather than the actual shift to the cued location (van Velzen and Eimer 2003). In the present study, however, the contralateral posterior component preceding saccades is triggered neither by lateralized aspects of the cue nor by a peripheral target, supporting the view that it is solely related to attentional shifts preceding the eye movement itself.

With regard to the potential neural sources of these attention-related contralateral ERP components, there is evidence that they both arise at least in part from parietal and occipital cortices (Hopf et al. 2000; Hopf and Mangun 2000). Investigations of the N2pc equivalent in monkeys performing visual search support this notion (Woodman et al. 2007) and, moreover, suggest that this posterior component partly arises from feedback of frontal eye field (FEF) neurons that are involved in voluntary attentional shifts (Cohen et al. 2009). While the present task is considerably different from covert visual-search paradigms, the observation of an N2pc-like distribution in the absence of a typical visual-search context appears to underscore that posterior regions are involved in the coding...
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M.G.W. interpreted results of experiments; R.M.K. prepared figures; R.M.K. drafted manuscript; R.M.K., C.N.B., H.H.Z., M.A.S., and M.G.W. edited and revised manuscript; R.M.K. and M.G.W. approved final version of manuscript.

ACKNOWLEDGMENTS

We thank Tineke Grent-'t-Jong for technical support.

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[PubMed: 18217799]


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**Figures and Tables**
Paradigm and behavioral results. A: participants performed saccades from square to square along the horizontal meridian guided by instructional color cues. The color cues (300-ms duration), which appeared at the currently foveated square, signaled the direction of the next saccade (e.g., green = right vs. red = left) or to maintain fixation (e.g., blue = maintain fixation) in the current trial. After each saccade, the participants' gaze remained at the new square until the next color cue appeared. SOA, stimulus onset asynchrony. B: saccade vectors were oriented either toward (centripetal, depicted in red) or further away from (centrifugal, depicted in green) the primary position (defined as head-centered straight gaze) and are described by specific start and end positions (start-to-end, e.g., 1-to-0). Note that 5 positions were required to enable the comparison of 1-to-0 centripetal (recentering) saccades and 1-to-2 centrifugal saccades that were matched for starting position and directional probability (filled arrows: main comparison). C: on average, saccadic reaction times (SRTs, collapsed across leftward and rightward saccades) were significantly shorter for 1-to-0 centripetal (red) compared with 1-to-2 centrifugal (green) saccades (*P < 0.005). Error bars depict SE across subjects. Note that the actual statistical test, as typical in repeated-measures designs, was based on the SE of the difference between each within-subject pair. SRT distributions for the conditions of interest are displayed in 20-ms bins at bottom.
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